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CONTENTS

PAGE

Special Review. **John Ford.** Research on populations of *Tribolium confusum* and its bearing on ecological theory: a summary . 1

Hugh Boyd Watt. On the wild goat in Scotland. With supplement: Habits of wild goats in Scotland, by **F. Fraser Darling** . 15

Gladys Keay. The ecology of the harvest mite (*Trombicula autumnalis*) in the British Isles 23

Dennis Chitty. A ringing technique for small mammals . . 36

Walter Pickles. Populations, territories and biomasses of ants at Thornhill, Yorkshire, in 1936 54

David Lack and **L. S. V. Venables.** The heathland birds of South Haven Peninsula, Studland Heath, Dorset 62

L. S. V. Venables. Bird distribution on Surrey Greensand heaths: the avifaunal-botanical correlation 73

D. F. W. Baden-Powell. On the Holocene marine fauna from the implementiferous deposits of Island Magee, County Antrim . 86

John Ford. Fluctuations in natural populations of Collembola and Acarina 98

Tom Warwick. The occurrence of disease among muskrats (*Ondatra zibethica*) in Great Britain during 1934 112

K. A. Pyefinch. The fresh and brackish water of Bardsey Island (North Wales): a chemical and faunistic survey . . . 115

Harold M. Hefley. The relations of some native insects to introduced food plants 138

J. S. Colman. The present state of the Newfoundland seal fishery . 145

J. E. Duffield. Notes on some animal communities of Norwegian Lapland: an account of the dung and carrion communities and of those insects found in human dwellings. 160

Averil M. Lysaght. An ecological study of a thrip (*Aptinothrips rufus*) and its nematode parasite (*Anguillulina aptini*) . . 169

E. Carey and **C. Diver.** Territory in the yellow field ant (*Acanthomyops flavus*). 193

Reviews 195

Notices of Publications on Animal Ecology 204

British Ecological Society. Reports of meetings, list of members, etc. 222

VOLUME 6 MAY, 1937 No. 1

SPECIAL REVIEW

RESEARCH ON POPULATIONS OF *TRIBOLIUM CONFUSUM* AND ITS BEARING ON ECOLOGICAL THEORY: A SUMMARY

BY JOHN FORD

(*Hope Department, University Museum, Oxford*)

(*With* 1 *Figure in the Text*)

THE series of studies on populations of the flour beetle (*Tribolium confusum* Duval), which this paper is intended to summarize, was initiated by R. N. Chapman (1928). Previously, this beetle had received considerable attention from entomologists (including Chapman), chiefly on account of its importance as a pest in stored cereals. Park (1934) has summarized most of the important facts connected with the general biology of *Tribolium*, and the following is intended to supplement his paper, on which, for the sake of completeness and to serve as an introduction, the remarks in § 1 are based.

1. Beetles of the genus *Tribolium* belong to the family Tenebrionidae, subfamily Ulominae. All members of this subfamily occur either as pests in stored products or else under the bark of trees and in rotting logs, and the two flour beetles, *T. confusum* Duval and *T. ferrugineum* Fab. (= *castaneum* Hbst.), have also occasionally been taken in these situations (Good, 1933). *T. confusum* can exist in a variety of cereal products, though not on the whole grain. Sweetman & Palmer (1928) have shown that vitamin B, which is present in most flours, is essential for its development. Good (1933) concluded that there might be from 6 to 11 larval instars, 7 or 8 being the most usual. Park summarizes Brindley's (1930) data on larval sizes and lengths of stadia and gives admirable figures of larvae, pupae and adults. Sex is easily determined in the pupal stage. The adults are reddish brown in colour and darken with age; their mean length is 3·4 mm.; males weigh on an average 1·48 mg. and females 1·78 mg. The period of development varies considerably according to conditions of temperature and humidity. Brindley (1930) found that the average was 30 days, from egg to adult, at 29° C. and 73 % relative humidity (R.H.). The adults have a relatively long life, again varying with environmental conditions but averaging about a year when these are favourable.

Park also deals with those papers which throw further light on the general biology of the beetle, particularly those of Chapman (1928) and Holdaway (1932), but they may more properly be considered separately in relation to other work on population problems with which he was not concerned in his paper.

2. Chapman (1928) first considered a fundamental property of natural populations which, by way of analogy, is stated in terms similar to those used for the relationship between electric current, potential and resistance as follows: "the quantity of organisms which may be found is the result of the balance between *biotic potential*, or the potential rate of reproduction, and the environmental resistance." On the basis of this hypothesis two experiments with *Tribolium confusum* were devised.

(*a*) The first was to test "whether a condition of equilibrium would be reached in which the population, as expressed in the number of individuals per gram of flour, would remain constant regardless of the size of the environment". A series of environments was set up of 4, 8, 16, 32, 64 and 128 g. of whole-wheat flour, the depth of flour in each case being the same. Into each environment adult beetles, one pair (male and female) to every 4 g. of flour, were introduced. Temperature and humidity were kept uniform. By using sieves of bolting silk of various meshes it is possible to remove eggs, larvae, pupae and adults from the flour separately. Counts were made at intervals of the numbers of the various stages present, and it was found that in each environment there was initially "a rapid increase in numbers, which was followed by a condition of relative stability.... The mean number of individuals per g. of flour in all environments after the attainment of stability was 43·97" $\pm$ 2·88. Thus the first proposition was verified. "A condition of equilibrium is attained in which the biotic potential is equalled by the environmental resistance and the population remains relatively constant," continuing with regular fluctuations in its various components, about a steady mean.

(*b*) Secondly, Chapman desired to test "whether the effective rate of reproduction of single pairs of beetles was inversely proportional to environmental resistance, which, in this case, is a function of the total size of the environment". A single pair of newly emerged adults was placed in each of a series of environments having the same quantitative relationship with each other as those in the first experiment. "In this case, in the same period of time, one pair of beetles gave rise to 178 individuals in an environment of 4 grams and another to 4500 in 128 g. The intermediate environments had populations of intermediate sizes." Within the period of the experiment only the smaller environments had reached equilibrium, with the same number of individuals per g. of flour as in the first experiment, while the larger environments were showing similar trends. Thus it was claimed that "the increase of a population is proportional to the size of the environments and, therefore, inversely proportional to the environmental resistance". It was, however, demonstrated by Allee (1931) and Park (1932) and also independently by MacLagan (1932) that, for the early stages of population development in *Tribolium*, this conclusion was not valid. These studies will be considered below. However, as regards the maintenance of the final asymptotic population, Chapman's explanation of the mechanism of environmental resistance is undisputed. He

showed that the adults and larvae are cannibalistic, eating eggs and sometimes young larvae and pupae. The frequency with which eggs are eaten depends on their relative abundance in the population. The number of eggs present in the population represents its biotic potential. "A high potential is ever present" but is prevented from realization in the balanced population by egg eating, "and when the environmental resistance" (egg eating) "is lowered by the death of adults, eggs hatch and produce new adults to take the place of those which have died".

3. Gause (1931) analysed Chapman's data and showed that the growth of the *Tribolium* population takes the form of the Verhulst-Pearl logistic curve (see Pearl, 1925). Further mathematical studies of *Tribolium* populations have also been made by Stanley (1932, 1932 *a*), who considered individuals in the population as "moving or stationary particles amenable to the formulations of the kinetic theory of gases" and was able to obtain theoretical curves showing "substantial agreement with the biological data". The present writer is unable to do more than notice these papers (the mathematical reader should consult them himself), but it is still necessary to emphasize the importance to ecologists of exact quantitative methods in dealing with animal populations, so amply vindicated by the results of the researches now under discussion.

4. Before passing on to a consideration of the relationship between population density and rate reproduction and to the effect of conditioning of the environment on the asymptotic population, it is necessary to examine the work of Holdaway (1932) in which further light is thrown on the effect of environmental changes on environmental resistance. Holdaway investigated the growth of populations of *Tribolium confusum* under different conditions of R.H. He found that the magnitude of the asymptotic, or balanced, population varies according to the amount of atmospheric moisture in the external environment, there being an optimum condition at about 75 % R.H. Above this level of humidity the balanced population decreases in magnitude as saturation is approached and, with complete saturation, reaches zero owing to the formation of fungi which prevent development. By maintaining a population at 25 % R.H. until it had stabilized itself and then transferring it to an atmosphere of 75 % R.H., he was able to show that population growth recommences in the new environment and continues until it has reached a higher level of stability. Further, it was shown that the rate of growth of the population increases with humidity, although the effect of humidity changes on the various stages of development of the beetles was not the same. The "viability of the eggs and pupae is at a maximum at low humidities, while for larvae it is at a minimum. As regards the duration of the various stages there is little effect on eggs and pupae.... The larval stage is the one in which duration is most affected by atmospheric moisture. It increases with decrease in humidity." It is not possible to summarize here all of Holdaway's results. They demonstrate the necessity of studying development as a whole in relation to environmental

change; that, in fact, studies on the effect of environment on separate stages in an animal's life do not necessarily indicate what the ultimate effect will be on the whole population. Of particular importance, however, in relation to the size of the balanced population is the eating of eggs and pupae. Holdaway suggests that the feeding stages of *Tribolium*, i.e. larvae and adults, may utilize the non-feeding stages, i.e. eggs and pupae as sources of moisture. This might account for the increase in size of the asymptotic populations with increasing humidity; for at 75 % R.H. the flour itself contains more moisture than at 25 % R.H., and consequently there is less need for larvae and adults to feed on eggs and pupae, and therefore a greater survival of these stages. He succeeded in showing that the percentage survival of eggs after 10 days of population growth at 75 % R.H. was 81 and after 30 days 54. The corresponding figures for a population kept at 50 % R.H. are 70 and 41. "It can then be affirmed that the mechanism by which atmospheric moisture regulates *Tribolium* populations is an alteration in intensity of the normal biotic control which the species can exert on itself; or in other words, the effect of the physical factor, humidity, on the insect population is *per medium* of a biotic effect, the intensity of which is regulated by the physical effect of atmospheric moisture on the moisture content of the flour."

5. We may now turn to the work of Park (1932), following Allee (1931) and MacLagan (1932). Chapman (1928) gives data for the density of beetles in six environments of 32 g. of flour each, which had been started with 1, 2, 3, 4, 8, 16 and 32 pairs of beetles respectively. All these populations reached equilibrium with density the same as in the experiments described. The three workers mentioned above re-analysed this data and found that in the earlier stages of population growth there is an optimum density for rate of reproduction. Park (1932) and MacLagan (1932) repeated the experiment and confirmed the results of these calculations. The rate of increase of a population of *Tribolium* can be expressed as the "progeny per beetle per day" or as "eggs and/or larvae per female per day". The following is taken from MacLagan's (1932) Table 1 and is recalculated from Chapman's data:

Beetles per g.	0·062	0·125	0·25	0·5	1·0	2·0
Progeny per beetle per day (11 days)	1·59	3·90	3·18	2·82	2·36	1·82
Progeny per beetle per day (23 days)	1·56	3·80	3·0	1·56	1·04	0·80

It is quite clear from this table that populations having an initial density of 0·125 beetles per g. of flour reproduce more rapidly than those with either lesser or greater densities. In Park's repetition of this experiment the result was essentially similar to that given above, with the optimum for reproduction rate at an initial density of 0·125 beetles per g. MacLagan's result, however, has additional interest in that his experiment was performed under somewhat different environmental conditions at 30° C., instead of 28° C., and at a some-

what higher humidity. In plotting reproductive rate against initial population density he obtained a curve of essentially the same form as Park's but the optimum had shifted to an initial density of 2 beetles per g. In commenting on this result MacLagan remarks that "in this instance, at least, the changed optimum density was not due so much to a difference in physical environmental factors (although perhaps partly so) as to the evolution of a strain of beetles which were not only better adapted to withstand crowded conditions but actually found the conditions of life under such circumstances more agreeable". This is of importance in that it indicates a factor, the ignoring of which has occasionally given rise to needless controversy. The behaviour of a *Tribolium* population depends not only upon the immediate conditions of the experiment but also to a large extent on the previous history of the individuals composing it. MacLagan's stock culture had been maintained for 6 months before the experiment under conditions of intense crowding.

It is now necessary to consider the explanations put forward for the existence of an optimum density for rate of reproduction. Park (1933) suggested that it arose from the interaction of two factors; the first, egg-eating, which is most intense in cultures of high density, and the second, the stimulating effect of copulation on the frequency of egg production. He found that the fecundity of females which had been associated with a large number of males was greater than that of females of the same age which had had only limited opportunities for copulation. This factor alone would tend to give populations of high density a greater rate of reproduction. On the other hand, the denser the population, the greater the amount of egg eating. This would tend to produce successively decreasing reproductive rates in dense populations. The two factors together combine to produce a maximum reproductive rate at an intermediate density.

MacLagan (1932), however, put forward other suggestions to account for this optimum density and carried out experiments to analyse its effect in populations of the grain weevil, *Sitophilus* (*Calandra*) *granarius*. This insect differs from *Tribolium* in that it feeds on the whole grain. Its eggs, "instead of being distributed at random in the floury medium, are inserted into the grains of the particular cereal being used".

Experimental environments were set up with 0·25, 0·5, 1·0, 2·0, ..., 32·0 weevils per g. of wheat grains. In each environment the numbers of males and females were equal. After 64 days the populations were counted and the increase in each expressed in terms of adult progeny per weevil. From these results it is seen that "the two variables, population density and progeny per weevil, exhibit a hyperbolic relationship". It is pointed out, however, that "to be strictly correct, the environmental unit of space, so far as oviposition is concerned in *S. granarius*, is *the number of available grains* per female weevil rather than the total volume per weevil". Thus the progeny per weevil in each environment is also plotted against the initial number of grains available. It is

found that the relationship is not rectilinear and it becomes evident that "although the progeny per female weevil decreases as the number of grains at her disposal decreases, she utilizes a greater percentage of the total available number, that is, the less space available the more efficiently does the female weevil utilize it, so far as oviposition is concerned, at least up to a certain degree of crowding". Beyond a certain point, however, the amount of oviposition continues to decrease until it ceases altogether when the density is 4 female weevils to one grain in a population of equal numbers of males and females. It is suggested that this change in the amount of oviposition occurs when crowding is such that it causes "undue interference in the act of oviposition resulting from repeated physical contacts".

Another fact which emerges from these experiments is that "the densities productive of maximum oviposition and maximum space utilization for the latter purpose, are by no means synonymous". Female weevils only laid the maximum number of eggs when the number of available grains was eight times that actually utilized. This occurs when there are 400 grains per female weevil. Maximum space utilization, however, occurs at 12·5 grains per weevil, though even then only 50 % of the grains are used. Further, it was found that if the number of grains per weevil was increased beyond 400 (where the greatest rate of reproduction occurred) there followed a reduction in the number of progeny, thus clearly indicating an optimum density for rate of oviposition.

In pursuit of further understanding of the density effect MacLagan tested the effect of one species upon another when both inhabited the same environment. As before, the weevil *Sitophilus granarius* was used, this time in conjunction with the moth *Sitotroga cerealella* which also breeds in wheat. Knowing from previous experiments the biotic potential of the weevils at different densities it is possible in these experiments to express the result of interspecific action as the percentage reduction in progeny per weevil caused by the presence of the moth. In original environments of 1000 grains the following result was obtained:

Weevils	Moths	Percentage reduction in expected progeny of weevils
10	20	24·0
10	40	8·3
40	10	Negligible

The interest of these figures lies in the fact that in no instance does the moth produce as great a reduction of progeny as would have been produced by an equivalent number of weevils. "Thus whatever the ultimate nature of the factor responsible for these reactions, it is not species specific, so that the effect can be brought about through the presence of other species in the environment, despite the absence of direct competition for food or oviposition space."

Another experiment in which the total volume available to the weevils was increased by the addition of glass beads to the wheat grains, in equal numbers,

thus doubling the volume while leaving oviposition space unaltered, gave a negative result.

Before discussing the conclusions of these experiments it is necessary to note a further publication, that of MacLagan & Dunn (1936). In the paper summarized above it was pointed out that the frequency of copulation might be affected differentially by crowding. Accordingly these workers carried out experiments with another grain weevil, *Sitophilus oryzae*. Six-hourly observations were made each day for 5 days of the number of females *in copula* in cultures of different densities. The results summarized below are extracted from their Table 1.

Weevils per grain	0·005	0·02	0·04	0·08	0·64	1·28	2·56
Percentage females (*in copula*)	22·8	31·97	33·06	24·23	5·89	2·56	2·01

This table clearly indicates an optimum density for copulation frequency. This optimum can be shifted by altering the physical or biotic factors in the environment. "For instance, by halving the number of males, the optimum is shifted to a more intense degree of crowding", and "by doubling the number of males the optimum is shifted to a less intense degree of crowding".

Further experiments with *Sitophilus oryzae* on the effect of density on oviposition confirm the results obtained by MacLagan (1932) with *S. granarius*. The rate of oviposition decreases continuously, in hyperbolic form, from lower to higher densities.

MacLagan & Dunn reach a conclusion which is paralleled by Holdaway's remarks concerning optima for the different developmental stages of *Tribolium*. "Living organisms are not always the highly coordinated physiological units they are often represented to be...and some should be regarded as heterogeneous assemblages of diverse physiological processes, each with its own optimum, rather than harmonious physiological units." Thus with the grain weevils copulation, oviposition and space utilization all contribute to the amount of reproduction and all find their maximum manifestation at different densities. MacLagan and Dunn conclude that the operation of density on population activity is largely through the medium of thigmotropism and is thus automatic.

Commenting on Park's (1933) explanation of the *Tribolium* optimum for reproduction rate MacLagan & Dunn remark that he "overlooked the possibility of a decreased copulation frequency above a certain degree of crowding, although this provides the key to the situation, as the decrease in population is greater than can be completely accounted for by eating of the eggs".

6. Turning once more to *Tribolium* studies we must note a paper of Chapman & Baird (1934). The purpose of these authors was to determine whether the behaviour of such populations is sufficiently constant to warrant "the biotic constants" of the beetle, such as time of hatching of eggs, duration of larval and pupal life, amount of oviposition, egg eating, etc., being used in

mathematical calculations. Running series of parallel cultures they found that the variations between them were small and that the biotic constants obtained were "sufficiently exact to warrant the use of mathematical formulae for calculating the potential trends of the population". They criticize Park (1933) in that his results differ numerically from their's and also show a higher degree of variation. Park, however (1935), has answered this criticism. "Why should the beetle populations of Park, most probably genetically different from those of Chapman and undoubtedly under certain different ecological conditions, give the same 'biotic constant' of reproduction as do those of Chapman?" It has already been noted that the previous history of the population is a factor which must be taken into account in describing population behaviour. We may note a remark of Tippett (1931) which emphasizes a fact often ignored by biologists. "In the biological sciences, the measured quantities are subject to uncontrollable variation", but "the statistician regards his variations as being essential properties of the population and they are as real as the average is." Thus we may note that if there are differences in the average values obtained in two populations having different histories, we may equally expect that the variabilities characterizing those average values will also differ. It is necessary to determine "biotic constants" afresh for each different stock of *Tribolium* used.

7. We are indebted mainly to Park (1934*a*, 1935) for our knowledge of another aspect of *Tribolium* populations. Recalling Chapman's original paper, it was shown that a population of *Tribolium*, whatever its original condition, ultimately reached a condition of stability with a density of 43·97 individuals per g. of flour. This stable condition is only maintained if the floury medium is renewed at fairly frequent intervals. If the flour is not renewed the activities of the beetles in producing excreta, etc., changes its composition and this has a deleterious effect on the population. The flour becomes "conditioned" and with increasing "conditioning" the population decreases and ultimately dies.

Park (1934*a*) first investigated the effect of conditioned flour on reproduction. 18 environments of 32 g. of conditioned flour were set up with one pair each of adult *Tribolium* of the same age and history. The conditioned flour had been previously populated by all stages of the beetle for a period greater than two life cycles. As controls 18 environments were set up, identical with the first set, save that the flour was fresh. Counts were made every 10 days, at which times the flour in the controls was renewed. The eggs and larvae produced were removed at each counting. It was found that whereas the controls maintained a constant level of productivity, the experimental populations produced a decreasing number of offspring at successive counts. Moreover, the initial production of offspring, for the first 10 days was lower than that of the controls. After 10 days two-thirds as many eggs were produced in the conditioned flour as in the fresh; after 60 days, only one-ninth as many. Since, however, the relative proportions of eggs and larvae present in experimental and control stock were the same, it is evident that infertility of eggs is not

responsible for the reduction in rate of reproduction. It may be due either to increased egg eating in conditioned flour or else to a decrease in fecundity of the beetles. Before passing to that question, however, we have to consider a second experiment designed to test whether "these experimental beetles may be returned to normal conditions by their return to fresh flour, or, are their reproductive processes so permanently inhibited that the number of eggs thereafter produced will remain permanently few?"

The same populations were used as above, but the experimental beetles were now transferred to fresh flour and for 40 more days were subjected to the same treatment as the controls, with changes of fresh flour every 10 days. At the 100th day they had reached nearly the same level of productivity as the controls, having commenced to increase their output of offspring with the change to fresh flour at 60 days. Meanwhile it became noticeable that the productivity of the controls had decreased slightly, an effect to be correlated with ageing of the parents.

Park (1935) next tested the effect of conditioned flour on egg-eating. 40 male beetles which had lived for 15 days following emergence in fresh flour were placed one each in 40 bottles containing 32 g. of fresh flour with 30 eggs randomly distributed in it. Another 40 bottles were set up in the same way, but with conditioned flour, the beetles in this case having passed 15 days since emergence also in conditioned flour. On the tenth day counts were made of the number of eggs remaining in each bottle. The eggs in each bottle were again made up to 30, the flour in the fresh flour bottles was renewed and the process repeated every tenth day for 50 days. The result showed that the beetles in the fresh flour consumed twice as many eggs, on an average, as those in conditioned flour. Evidently, then, egg eating cannot account for the reduced rate of reproduction in conditioned environments. "It may be that conditioned flour lowers the general physiological level of the organism and thus reduces its food intake." Or, on the other hand, eggs may be more difficult to locate in the conditioned flour.

The reduction of the population in the latter medium must then be due to a decrease in fecundity of the females. This was shown as follows. Virgin females are able to lay eggs, which, owing to the absence of copulation and, hence, fertilization, are infertile. The average number of eggs laid by virgin females in 5 days, in fresh flour, was 50·3; in conditioned flour, 16·8. An experiment with mated beetles yielded similar results. Egg counts were made daily in 20 sets containing single pairs of fresh-flour beetles and likewise with a similar set of conditioned-flour beetles. At each count the eggs were isolated in order to test their fertility. The egg rate per female per day in fresh flour was 1·5; in conditioned flour 0·17. Further, it was shown that egg laying by the conditioned-flour females was extremely erratic, and it seems evident that the organisms "are fundamentally influenced by such conditioning". A continuation of the experiment in which the type of flour supplied to the beetles

was reversed showed that conditioning does not "irrevocably alter the fecundity of *Tribolium*", a conclusion to be expected in consideration of Park's earlier experiment, concerning the recovery of a conditioned population when returned to fresh flour.

Park (1935) now tested the effect of male conditioning on fecundity. In environments similar to those described above he made the following matings:

Fresh-flour male × fresh-flour female.
Fresh-flour male × conditioned-flour female.
Conditioned-flour male × fresh-flour female.
Conditioned-flour male × conditioned-flour female.

The conditioned-flour females had low egg rates irrespective of the history of their mates, but while both the fresh-flour females had high egg rates, there was a significant difference between them, the fresh-flour females mated with conditioned-flour males having lower rates than those with fresh-flour males. A conditioned-flour male can, then, affect the fecundity of a fresh-flour female.

In examination of the isolated eggs mentioned above it was found that there was no significant difference in fertility between fresh-flour eggs and those from conditioned-flour females. However, examination of the larval stages through which fresh-flour and conditioned-flour larvae pass makes it quite clear that conditioning greatly increases the mortality of metamorphosis as well as slowing down the rate of development.

The conditioning of the flour, i.e. the alteration in the composition of the environment by the activities of the population inhabiting it, is therefore of great importance in controlling the abundance and length of life of the population as a whole. The exact nature of the physiological effects of conditioned flour, which produce these changes in the behaviour of individuals, is not yet known. It has been shown, however (Park, 1936*a*), that the decrease in fecundity produced by conditioned flour is not "symmetrically proportional" to the amount of conditioning. This was shown by testing the fecundity of beetles in varying mixtures of fresh and conditioned flour. There was no significant difference between the fecundities of beetles in environments with $\frac{3}{4}$ fresh and $\frac{1}{4}$ conditioned and $\frac{1}{2}$ fresh and $\frac{1}{2}$ conditioned flour, though both were intermediate between entirely fresh and $\frac{3}{4}$ conditioned and $\frac{1}{4}$ fresh flours.

As a first step in the investigation of *Tribolium* physiology Park (1936) has shown that conditioned flour has no appreciable effect on the oxygen consumption of individuals, although it is shown that females require more oxygen than males, a fact possibly to be correlated with their greater weight.

8. To turn now to an entirely different aspect of the *Tribolium* researches we come to the work of Chapman (1933) and Chapman & Whang (1934). The work of Gause (1934) has now popularized our knowledge of competition fluctuations in animal population, and there is no need to discuss their mechanisms here.

In a population of *Tribolium* initiated with a small number of adults the following changes take place. First there is a steady increase in the number of eggs present. After some days (the exact period depending on the physical conditions) the first laid eggs begin to hatch and there follows an increase in the number of larvae, and coincidentally with the increase in larvae there is a decrease in the number of eggs present. The next stage is that in which the larvae commence to pupate, and the pupa population increases simultaneously with a decrease in the population of larvae. The egg population again rises, and now pupae begin to hatch producing an increase in the adult population which eventually reaches a steady state, while larval and egg populations continue to fluctuate about a stable mean. These fluctuations are best explained by treating the larvae and adults as predators of the eggs, which are themselves being

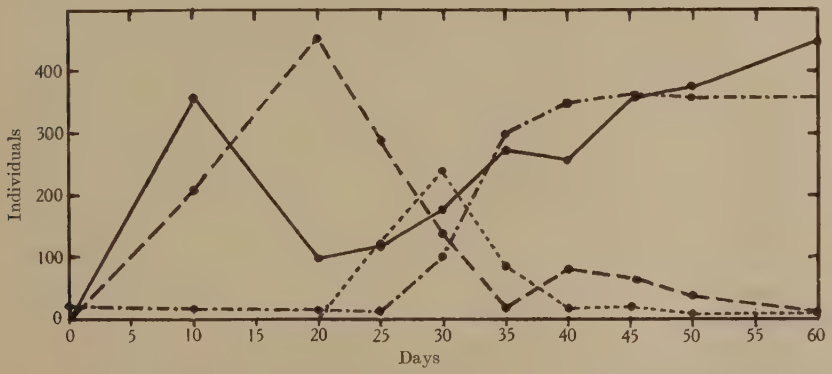

Fig. 1. Population trend of *Tribolium confusum* at 32°C. and 75 per cent. R.H. Eggs ——; Larvae — — —; Pupae - - - -; Adults — · —.
(Redrawn, by permission, from **Chapman** (1931), *Animal Ecology, with especial reference to insects*, p. 213.)

produced by the adults. Thus the first decrease in eggs takes place when the larvae hatch, and it continues, owing to the predatory action of the larvae, until the larval population is reduced by pupation, which, of course, allows the egg population again to rise (Fig. 1).

Confirmation of this view is obtained in experiments described by Chapman (1933). The Sporozoon *Adelina* is parasitic in *Tribolium* larvae, causing their death during the instar immediately preceding pupation. Thus in parasitized cultures no adults are produced, and the population gradually declines owing to the natural death of adults and the consequent failure to maintain the egg population. During this decline the populations of eggs and larvae fall into fluctuating rhythms which alternate with one another. Eggs are continually being produced by the surviving adults thus *tending* to an accumulation of eggs. Meanwhile larvae hatch from the eggs, on the remainder of which they

feed. There is here the mechanism of fluctuations between predator and prey of the Lotka-Volterra type, and such fluctuations were found to occur in both accidentally and experimentally parasitized cultures. The parasite, by removing the pupal and adult stages from the population. has the effect of once more starting the larva-egg fluctuation with which a *Tribolium* population commences.

Inasmuch, however, as Park (1932) and MacLagan (1932) had demonstrated that there is an optimum for oviposition at low densities, it is possible that the initial decline in the egg population may be due to a decrease in oviposition following an increased density due to the presence of larvae. Chapman & Whang (1934) set up artificial populations composed entirely of males to which they added eggs at constant rates equivalent to the egg-laying rate in normal populations of the same size. There was here a constant "oviposition" rate. They found that the decrease in the egg population coincident with the hatching of larvae took place exactly as in a normal control culture, save that the peak in the egg curve was slightly higher than the controls. It is possible, however, that although the difference between experiment and control was within the limit of statistical error, the slightly lower value for the control was due to a decrease in oviposition. But whether this is so or not, Chapman & Whang have clearly demonstrated that egg consumption by larvae is responsible for the main trend of the egg population, in the early stages.

It is necessary to note here that this account of fluctuations in *Tribolium* populations is probably too simplified. Considerations of space have made a full discussion impossible, but it may be noted that since fluctuations imply changing densities it is probable that in addition to the egg-eating factor (which itself needs further analysis) differential crowding effects on reproductive rates at successive phases of the fluctuations, must also be taken into account.

Prof. Chapman has kindly informed the writer that the populations mentioned in his paper (1933) have now maintained synchronous fluctuations over a period of approximately 5 years, and that he and his associates have carried out further experimental analyses which should throw more light on this complex problem.

Summary and Conclusions

To conclude, we may review briefly the chief characteristics of natural populations as seen in the light of such studies as those here discussed.

In its growth the population tends to take the form of the logistic curve (Pearl, 1925). This curve expresses a tendency to geometric increase which is less and less realized as the population approaches saturation, owing to the increase in environmental "resistance" with increasing density. Such a form of population growth is only manifested in unmodified form under constant physical conditions and where there are no interspecific effects. In nature a variable physical environment causes modifications which are brought about in

many ways. In *Tribolium* it has been shown that alteration in the external environment may change rates of growth, perhaps with opposite effects in different stages of the life cycle; it may likewise affect the amount of crowding which represents the optimum for rate of increase of the population. Under constant conditions any population imposes on itself a limit to increase and eventually reaches a state of relative stability about which it fluctuates. With a natural population which has reached equilibrium, changes in the physical environment may alter the value of this stable density and the population proceeds to readjust itself. Alternatively, the population itself, even when external conditions of temperature, humidity, etc., are constant, may so alter the environment by its own activity as to make yet other disturbances of the equilibrium. Provided the environment is such that the species concerned is able to live and reproduce in it, the factors *immediately* controlling the growth and behaviour of its population are biotic and proceed either from within the population itself or from without by the action of competing species. These biotic factors are themselves modified in intensity or in kind by external changes in physical factors.

It is the task of the ecologist first to assess the values of the physical environment in altering the behaviour of populations by its effect on individual and communal activity, and secondly, to interpret population phenomena in quantitative terms of increase and decrease in relation to intra- and interspecific competition. Population studies on various insects, mites and Protozoa (Gause, 1934) have greatly enlarged our knowledge of these phenomena. It is to be hoped that the value of this knowledge may be increasingly realized and put to use in quantitative field studies, and that soon it will be no longer necessary to agree with Gause that "as yet to many ecologists the ideas of biotic potential and environmental resistance are not connected with any quantitative conceptions".

ACKNOWLEDGMENTS

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ON THE WILD GOAT IN SCOTLAND

By HUGH BOYD WATT

With Supplement

HABITS OF WILD GOATS IN SCOTLAND

By F. FRASER DARLING

(*With Plate* 1)

This paper is offered as illustrating a by-way in Scottish natural history, showing how domesticated goats have run wild or become feral in a country to which the species was introduced by man in early times. Along with the sheep and ox, it was amongst the first introductions of what may be called utility animals. The goat, in the course of time, apparently proved to be one of the least useful, and many seem to have been allowed to run wild or were turned loose. Pennant (**7**), writing more than 170 years ago, remarks that the goat is the "most local of our domestic animals, confining itself to the mountainous parts of these islands".

Herds of goats which used to be maintained have not been kept up; an English instance of this is the old-established herd in Bagot's Park (Needwood Forest), Staffordshire, which has dwindled within memory from 200 animals to about 60. The goats are said to be now very wild and only seen at rare intervals.

In many parts of the world domesticated goats have reverted to a feral state as in Scotland and the Hebrides, Wales, the Canaries, Azores, Ascension, St Helena and Juan Fernandez.

The normal type of domestic goat is derived from the Persian or Grecian wild goat (*Capra hircus aegagrus* Erxleben), and from this form and cross-breeds the majority of domestic goats (*Capra hircus hircus* L.) have descended (**9**).

It is this form that is found in Scotland, and in a wild state it is generally but thinly distributed in some districts from the Shetlands to Galloway and the Cheviot Hills, the preponderance being in the Highlands and Western Islands. Information about several places is vague and particulars difficult to obtain, but the status and distribution of the animals are outlined in the following notes.

1. North Scotland and Central Highlands

From Sutherland there are few reports; but the Reay country and Abercorse near Loch Fleet are named. Mr Frank Wallace tells me that, years ago, in shooting he killed only one wild goat in Sutherland. The best head he knows is at Altyre (Roualeyn Gordon Cummings' "mascot"), and Mr Wallace mentions

Douchfour on Loch Ness, making the general remark that goats are pretty widely distributed in the Highlands. In North Morar (Inverness-shire) there is an old established herd, advertised as amongst the attractions of the estate when the deer forest was in the market in 1930, and Messrs Rowland Ward, Ltd. (**11**), record two heads from Meoble. Millais mentions the Morar hills as one of the districts in which he saw wild goats, and also Strathpeffer, Rothiemurchus and the Perthshire hills from Glen Lyon to Rohallion. This author and artist has a plate with two wild goat heads, one marked Sutherland (length of horn 33 in.) and the other Ross-shire (length of horn 36 in.) (**5**).

Goats were mentioned in 1835 as formerly numerous in the parishes of Glenmorriston and Urquhart, but discouraged as injurious to woods and plantations. This reason, joined to the antipathy which sportsmen have to the presence of goats on their shootings, indicates why wild goats in the Highlands are kept down. In Cromarty the Black Isle Cliffs are at present known as a haunt of wild goats. These may be the descendants of a flock of goats seen on the most inaccessible looking part of the cliffs by Charles St John, who lived in the Highlands from 1837 to 1853. He also saw an old goat and a pair of kids on the rocks near Cromarty. St John further describes goats seen by him on rocks at Bridge of Dulsie, Findhorn River, as long-horned, half-wild, with shaggy hair and long venerable beards. In Rothiemurchus, wild goats may now be out of existence, although Mr Seton Gordon tells me that up to the time of the War (1914) they were certainly on Creag Leth Choin. In the Cairngorm Mountains there are recent records from the slopes of Lochnagar, the Slochd and Glen Callater (Braemar). The goats of Callater have been photographed at about 3000 ft. above sea-level and kids seen. On Bennachie they are found in small numbers (**10**).

Coming to Perthshire, a story dating back to 1829 says that the "only novelty from the hills this season is the murder of half a dozen goats by an English party in Atholl, who had mistaken their prey for deer". In central Perthshire there was, and still may be, a herd on Schieallion; the fine bearded head shown in the Natural History Museum, South Kensington, marked "Scotland, 1894, presented by Sir Donald Currie", may be from that locality.

Ben Venue is frequented by goats perhaps descended from those mentioned by the poet Southey as "having become wild" (**10**). They have been known on Ben Venue from generations, and three heads of bucks shot from a flock at Achray, Callendar, are shown in Robert Wallace's work on "Farm Live Stock in Britain" (Plate CCXXII). A head from Achray is amongst the sporting trophies entered in Rowland Ward's book (**11**). Other Perthshire localities are Loch Lairig Eala, Glenogle, Glen Falloch, where herds of six to twenty have been seen (**12**) and Ledard near Loch Ard.

The goats of Inversnaid, on Loch Lomond, are reputed to possess a pedigree dating from the time of King Robert the Bruce, who ordained that these goats should never be molested (**10**). Goats are said to be quite common on the

slopes of Ben Lomond, and a tradition persists that wild goats were inhabitants of the yew-tree island, Inch Lonaig on Loch Lomond, and wrought destruction to the trees.

2. WEST HIGHLANDS AND THE HEBRIDES

Wester Ross is a great stronghold and Millais gives north-west Ross-shire as one of the districts where he saw wild goats, adding that there is always a herd in the Morar Hills (**5**).

The present writer is greatly indebted to Dr F. Fraser Darling of Dundonnell for first-hand up-to-date information given below, and also for his article on "Habits of Wild Goats in Scotland" (see Supplement).

Gruinard Forest has a long-established herd of from thirty to forty in number; coloured black, grey, and black and white; occasionally a good head is shot. In Fisherfield Forest there are a few of broken colours. On the north side of Strath Beag, Dundonnell goats of local origin were introduced in 1911 to add to the sport of the place: a mistaken idea. The mountain called An Teallach carries a small herd of about ten or twelve on the cliffs of the topmost thousand feet. The goats are pure white and the most magnificent of their kind that Dr Darling has ever seen. They have strong horns of a wide spread, very long thick coats and exceed in size any other wild goats in the West. On the north shore of Little Loch Broom, a crofter keeps goats of the wild type. At Kildonan (Badrallach) there is a flock of about forty owned by a shepherd and these are indistinguishable from wild goats. At Rhirevoch, further along the peninsula, is a herd of one hundred or more that run wild on Beinn Ghobhlach.

Another correspondent reports having seen about thirty goats on Dundonnell Hill, near Ullapool, in 1928 (**12**). There are other records from Loch Broom, and in Loch Ailort there is an island called Eilean nan Gobhar (Isle of Goats). A local story (**1**, p. 20) of the time of Prince Charlie (1745–46) tells of goats on this island, but only negative information is forthcoming at present.

Benderloch and Easdale are also named in an indefinite way, and a herd on Eorsa is said to have been kept mainly as a curiosity. In Morven, on Aonach Mor or Innean Mor, there were considerable numbers (fifty or more) many years ago, but no wild goats are now known there. On Aird-Ghobhar (Ardgour) there is said to be a "trip" of fifty or so.

Throughout the scattered islands of the Hebrides the wild goat is fairly well known. An early traveller, Martin (previous to 1697), says of the "Isle of Harries" that goats were in the Isle of Lewis. He repeats a story of the natives about "a couple of goats that did grow wild on the hills and after they had increased they were observed to bring forth their young twice a year" (**4**). In Lewis at Dune Tower (Ness) there were, in 1930, a goat or two left to their own devices, no doubt reverting to a state of wildness. The wild goats of Harris are described by Harvie-Brown (**2**) as having very fine heads and horns; he

gives a vivid description of the goats traversing cliffs which appear to the eye to be sheer precipices, and feeding on the grass and herbage growing in the crevices. The same writer mentions goats on Cara Island introduced previous to 1793, and on a small island close to Oronsay; also Ardmaddy previous to 1812 and Tiree and Coll (**3**). Cara has some white goats at the present time. Pennant (**8**) suggested in 1776 that in Skye goats might turn to good advantage if introduced to the few wooded parts of the island. "Skie", however, is mentioned by Martin (**4**) as "producing" goats amongst the "cattel" at the two fairs held each year. There are, amongst the specimen heads of wild goats in the Natural History Museum, South Kensington, two trophies of the white variety from Scalpay, Isle of Skye, dated 1895. Mr Seton Gordon says that he has seen goats above Suishnish in Sleat. Dr Darling reports his experience on Priest Island (see Supplement) and that there are a few goats of the wild type on Horse Island—both islands are in the Summer Isles.

In the island of Rum there is a nameless peak to which it is proposed to give the name of Sgurr nan Goibhrean (the peak of the goats) as wild goats are to be found there (**6**). The neighbouring island of Eigg has a mixed herd including a male from Holy Island (Arran) introduced in recent years. The idea of this was to see how long it takes a mixed population to assume a general wild type. Although food was provided, the animals only took it in the first winter and prefer to forage for themselves (**10**).

On Little Colonsay, west of Mull, there are ten or twelve goats running wild, introduced about 1922. They are grey, black and white and very good looking beasts (Dr Darling). On Staffa goats were known in 1802, but none now (**1**). To the island of Mull belongs the distinction of having yielded a head for the small collection shown at South Kensington and also the recognition of the wild goat for sport. In quite recent years goats were included, with other game, in the attractions of the shootings of Lochbuie in that island. There is a fine head in the hall of Maclaine of Lochbuie's house. Other places in Mull are Burg where there is an estate on which wild goat shooting was let and near Carsaig at the present day "wild goats spring from ledge to ledge of the great rocks that tower above" (**1**). Other places known in Mull by hearsay are Pennyghael, fifty to one hundred goats all or many alleged to be white; and Kilpatrick. It is possible that these, with the exception of the Burg herd, are all one and the same lot roving about. The neighbouring island of Ulva had what is called a "trip" numbering twenty to fifty, shy and agile, and mixed as to colour. An episode in their recent history is that they marooned themselves on a tidal islet in the Sound or Loch Tuath and, on attempting to return through a high tide and wind, about twenty out of twenty-five were drowned. There is a mounted head from Mull in the Natural History Museum, South Kensington. Martin (**4**) names goats in Mull under cattle.

Pennant (**8**), on his visit to the Isle of Jura, saw the shealings of goat-herds who kept a flock of eighty goats for their milk and the cheese made from it.

Photo G. H. Stevenson

White goats on Cara, 8 July 1935.

BOYD WATT—WILD GOATS

Face p. 18

At the present time this island carries very fine examples of the wild goat; the Royal Scottish Museum, Edinburgh, possesses a mounted specimen, cream coloured, presented by Mr Charles C. Campbell (**1**, **10**) taken in 1931, and a head, mostly black, taken in September 1922, presented by Viscount Astor. There is another head from Jura entered in Rowland Ward's MS. records as from Mr H. H. Williams.

In Islay three colonies of wild goats are known at present. The oldest is at Kinnabus on the Mull-of-Oa side of the island, said to have been in existence "from time immemorial". The other two colonies are on the west side of the island at Smaull near Kilchoman, numbering seventy, introduced from Kinnabus about one hundred and fifty years ago. The third lot is at Gortantaoid on Loch Gruinart, introduced from the islands of Mull and Jura about twenty-three years ago. This colony numbers about one hundred and fifty and my informant says that goats do very well on Islay and breed so freely that their numbers have to be reduced from time to time.

3. Clyde area

Coming to the Firth of Clyde, the Mull of Kintyre and Davaar Island are mentioned, but particulars are wanting. Of Ailsa Craig, we have records which run from Pennant's time (**8**) to the present date. The *Old Statistical Account of Scotland* (1791) states that Ailsa was uninhabited but that goats occurred there. About 1836, the tenant of the Craig "went there for a few days' shooting at the wild goats which abound". Goats continued to inhabit the island, and visitors to the tops frequently had glimpses of them. A head was received by Messrs Rowland Ward, Ltd., in 1935.

Word has recently been received that there are now no wild goats at all on Ailsa Craig, only tame ones (a herd fluctuating between twenty and forty). The wild ones were found to be troubling and molesting the tame herd which is kept for milking purposes, and they were therefore shot or allowed to die (letter 13 Oct. 1936 from Mr H. G. Vevers, Oxford, to H. B. W.).

Of Arran there are reports going back many years, and recent evidence of the presence of wild goats is that an animal from the island was amongst the material used by T. W. M. Cameron and Ivan W. Parnell in their paper on "Internal parasites of land mammals in Scotland" (1933, *Proc. R. Phys. Soc. Edinb.* 22: 141).

Holy Island (Arran) has as long a history as Ailsa, Pennant having seen goats there in 1772 (**8**). At the present time the animals frequent the rocky eastern slopes of the island and are fairly numerous. They are white in colour and it has been remarked that if they cannot always be seen they can usually be smelt (**1**, **10**).

In Bute there are two herds, one at the north end about forty in number in 1932; the second and smaller lot are at the south end near Garroch Head (**10**).

4. Southern uplands

In this part of Scotland one of the best known places for wild goats is near St Mary's Loch; localities named are Saddleyoke, Brandlaw and Meggat Water. The goats roam the hills and are not interfered with by the shepherds (**10**). In Ward's "Records" are entries of heads from near Moffat and from Cumloden (**10**). There are also records from Tarras Valley, Ewes parish, near Langholm of a herd of twenty; a buck shot had a head with a spread of about 4 ft. and this was in the possession of my informant for some years. In the Kells range, New Galloway, six wild goats were seen in 1912. From a recent newspaper report wild goats are becoming a regular nuisance in the Galloway Hills where pasture for sheep is none too abundant. They are very wild and difficult to approach but occasionally the sheep-dogs manage to kill one (**12**).

Glenapp and Cairnharrow at one time harboured goats but information as to the present time is wanting. Millais (**5**) names the Cheviot Hills as one of the places where he saw goats and Mr T. Russell Goddard has been successful in photographing them on the Cheviot.

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I desire to express my thanks to all who have given information and assistance and particularly to Dr F. Fraser Darling, Dundonnell; Mr D. Macintyre, Invergordon; Mr A. M. MacLachlainn, Tobermory, Mull; and Mr Archie Ferguson, Bridgend, Islay.

Summary

Goats, which have become feral, exist in many parts of Scotland, including some of the islands. This paper summarizes available information about the history and present status of these wild goat populations.

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HABITS OF WILD GOATS IN SCOTLAND

BY
F. FRASER DARLING

THE story of how goats became feral in Scotland would be an interesting one if it were fully known, for it is closely bound up with the affairs of men through a long period.

The goat is an able fellow and can go feral with no difficulty and in a very short time. The reversion to wild type is rapid and ten years can make a big difference in the general appearance of a herd. What, it might be asked, is the influence on nitrogen metabolism which makes feral goats run increasingly to hair and horns until the standard of the wild goat is reached? Natural selection must be a potent factor in levelling the type of goats newly gone feral. The breeding season is early and kids appear frequently in late January and February, which is no time for young things to appear in the West Highlands. This early breeding season serves as an extremely fine mesh sieve in preserving only those which suit the conditions. I have no figures on actual kid-rearing percentage in "wild" goats, but it must be small. This tends toward a stable population and it is worth remarking that the goats are distinctly local in their distribution, and there is little if any evidence of spread or extensive migration.

The crofter who keeps goats of the wild type on the north shore of Little Loch Broom has begun recently to catch up the bucks at the beginning of August and to keep them penned until November in order to overcome the early kidding problem.

I had some first-hand experience of the way in which goats go feral during the time I spent on Priest Island, Wester Ross, in 1936. We took two newly kidded goats of milking type to supply the family. The island is a much broken and very rocky place and the goats, normally quiet members of caprine society, have had the run of it. When newly kidded they came back night and morning to be milked. Two or three months later they came when they were called, sometimes from a considerable distance; but towards the end of their lactation, when their bags were never full enough to be uncomfortable, we had to go and hunt them each time. Furthermore, they took increasingly to climbing about the cliffs and sometimes we had to get them out of most awkward places. It is obvious that had we been on the mainland we should have had to tether the goats or they would have been away to the rocks for good.

Years ago, goats were used by the crofters much more commonly than now (though in this connection there are many more goats in current use in the Eastern glens by shepherds, stalkers and keepers than in the West Highlands). There is no doubt that my own experience must have been common —that with the decline in lactation, and as the goats grazed further afield as herbage coarsened in late summer, they got lost, or rather were not found, and gradually

became wild. Again, a great many goats went wild at the time of the clearances. The crofters were pushed out and in many cases they were unable to gather all their goats from the mountains. This applied particularly in the West where, as Mr Boyd Watt notes, there are many more feral goats than in the East.

The fine herd of pure white goats which lives on An Teallach, the precipitous mountain near my home, is a modern example of goats going wild. They are very wild indeed and almost impossible to stalk, and yet the foundation stock of this herd was owned by a crofter on the shores of Little Loch Broom as recently as ten years ago. Several herds of "wild" goats such as the one mentioned above, are nominally owned by crofters who have no claims on the forests in which the goats roam. This ownership is purely nominal, for the crofters could never get the goats and their descendants out of such places as the cliffs of An Teallach.

What is the life of the goats once they are feral? They are usually found on the higher reaches of the mountains and there is reason to think that it is not only love of high places which keeps them high but the fact that they dislike wet ground. The goats keep above the peat line (about 1700 ft. on An Teallach) where drainage is good and what ground there is other than rock is soon dried. It is perhaps unnecessary to say that the goats are perfectly intimate with their country, but the observer cannot fail to be impressed with the animals' movements about a rock face which has occasional sloping ledges of alpine herbage. A man may follow a deer path anywhere with complete safety, but certainly not a goat track. The goats never appear to be in a hurry and they seem well aware of their tactical position in relation to a human being. I have watched them often in the deer forests of Dundonnell and Gruinard. Sometimes the white goats of An Teallach have moved away from me across the face of the mountain and I have noticed that the buck leads the way and the nannies send their kids in front of them through the worst of the rocks. If the kid takes a step in the wrong direction it gets a dunt from its mother's horns as correction. The herd seems to be patriarchally governed throughout the year. A mature buck will have with him about half a dozen nannies and their kids of the year. Yearling bucks follow on the outskirts of the group.

"Wild" goats may see an approaching human being from a long distance but they do not raise their heads in alarm and rush away like sheep; they wait. It is probable that the observer will have to lose sight of them for a while in the course of his stalk because of the nature of the country. That is the time when the goats disappear. The observer will not have seen them go and it is highly unlikely that he will be able to find them thereafter.

THE ECOLOGY OF THE HARVEST MITE (*TROMBICULA AUTUMNALIS*) IN THE BRITISH ISLES

By GLADYS KEAY

(*Department of Zoology and Comparative Anatomy, University Museum, Oxford*)

(*With* 1 *Figure in the Text*)

CONTENTS

PAGE

1. Introduction 23
2. Distribution in the British Isles 24
3. Hosts (*a*) Summer 28
   (*b*) Winter 29
4. Rearing of the nymph 31
5. Geographical distribution of Trombiculae parasitic on man . 32
6. Summary 34
   References 35

1. Introduction

The harvest mite, *Trombicula autumnalis* Shaw, commonly known also as the "harvest bug", occurs in many districts in the British Isles. It belongs to a family of mites which is interesting in many ways. They escaped attention for a long time on account of their small size. But their importance as transmitters of disease in some parts of the world has led to more detailed investigations. The confusion which arose over their nomenclature owing to authors attaching a name to every larva and adult they found, irrespective of whether these were stages in the life history of the same animal, has provided scope for systematists. The work of the systematists cannot be completed until all the life histories are known, and this problem has attracted other investigators.

T. autumnalis itself has caused considerable difficulty to the systematists. André (1930, p. 60) gives a historical account of the systematic position allotted to this mite from 1876 to 1928. The larva alone was known until 1909 when Bruyant (1909*a*) reared the nymph (which he called *Microtrombidium pusillum*). In 1926 Hirst reared one nymph which he thought was the same as that reared by Bruyant, and in 1928 André (1930, p. 110) reared 14 nymphs. So far all efforts to rear the adult have failed; but in 1929 André (1930, p. 122) found a single specimen of what he thought to be the adult in the soil in Seine-et-Marne. *T. autumnalis* presents another interesting feature in its sporadic distribution. This is characteristic also of *T. akamushi* in Japan and *T. irritans* in the United States. No explanation has yet been given.

The present paper deals but briefly and only historically with the disease aspect of the *Trombicula* problem. It does not deal at all with systematics.

Its main concern is with the distribution of the harvest mite in the British Isles, and to some extent with the distribution of related species in the world. The hosts of the harvest mite are also recorded, and the habitats selected on those hosts. In addition an account is given of some breeding experiments in which nymphs were successfully reared.

I wish to thank Mr Charles Elton for his advice and assistance in this work, and also Mr A. D. Middleton for his assistance in field work, and for putting me into contact with many observers both in England and Scotland. My thanks are also due to Dr S. Finnegan for allowing me access to the collection of mites in the British Museum, and to Prof. E. S. Goodrich, F.R.S., for the facilities given me in his Department.

2. Distribution in the British Isles

The known distribution of *T. autumnalis* in the British Isles is shown in the accompanying map and Table 1. Information was received from many different sources. By the kind permission of the editors, notes and enquiries about the harvest mite were published in *The Times*, *The Manchester Guardian*, *The Scotsman*, *The Field*, *Country-Side*, *The Cornish Farmer and Auctioneer*, *The Scottish Naturalist* and *The Irish Naturalist*. My thanks are due to those people who answered the enquiries, and particularly to those who sent specimens. The replies are deposited in the Bureau of Animal Population at Oxford, and specimens are being deposited in the British Museum.

In many cases where the mites were actually seen they were found on animals. This is due to the fact that they occur in clusters, and form a bright orange patch which is easily seen. They do not cluster on human beings, and are difficult to see when solitary, hence many people who have suffered from their bites have never seen the cause of their discomfort. The bites always occur most abundantly where there is pressure from clothing, e.g. round the top of shoes, under garters, round the waist, and also under the knees and in the arm-pits. These positions are so characteristic that there is little doubt that those observers who describe bites alone are recording the bites of harvest mites. In a few cases conclusive evidence of their presence has been provided in the form of specimens. These were obtained from dogs, cats, rabbits, wood mice, voles and partridges.

From Ireland but few records have been received. These are shown on the map, but they cannot give anything like a complete picture of the distribution. The few observers lay stress on the great abundance of *T. autumnalis*, called by them the "Orange Tawny", in the districts in which they have made their observations, and cases have been reported of the irritation from bites being severe enough to cause slight fever.

There are a great many areas from which neither positive nor negative evidence of occurrence has been received. It is very difficult to prove conclusively the absence of any creature, particularly when it is as small as the larval

T. autumnalis, and negative evidence must be accepted with caution, even though the information is received from reliable sources. Records of absence have only been accepted from people who spend much of their time in districts where they would be almost certain to observe the harvest mites if they were present, e.g. farmers, foresters, estate agents, landowners and also competent naturalists. Even then there is the possibility that the observers are immune to attacks of the pest and have not noticed the mites for this reason. However, the records will probably show at least the places in which the harvest mite is rare if not entirely absent, for when prevalent it can scarcely escape notice.

It is interesting to note that several of those negative records come from the Weald, an area bounded on the north and south by chalk downs on which the harvest mite is rampant. In Yorkshire too they indicate that the mite is present in great numbers only on the Wolds, which are also chalk. Several observers from Dumbartonshire record the absence of *T. autumnalis*, but in the same region of West Scotland, on the island of Little Cumbrae, harvest mites have been found in vast quantities on rabbits, and are a serious pest to the inhabitants of the island in summer.

For rearing harvest mites one of the necessary conditions is sufficient moisture, and André (1930, p. 132) states that in nature they prefer clayey soil, especially when covered by humus, which retains a great deal of water.

In England most of the records come from calcareous soil. The preference for chalk seems to be strongly marked in some localities. A case is reported from Tillingbourne Valley, Surrey, where harvest mites are found in abundance on the chalk side of the valley but not on the sandy side. Prof. Salisbury, replying to the enquiry in *The Times*, stated that he had noticed the association of *T. autumnalis* with calcareous soil, or other soils which are low-lying and have been enriched by bases leached down from the high ground above. Instances of this were met with near Ilfracombe in Devon, and Wenlock in Shropshire.

My own investigations were done chiefly on the area surrounding West Ilsley, Berkshire. The soil is calcareous. A curious instance of the sporadic distribution of the harvest mite was met with in this district. In a certain valley on the downland there are numerous rabbit warrens, the runs of which are believed to be continuous. One day, early in May, 10 rabbits were secured in one area, and every one had harvest mites in its ears, while in another area about 100 yards farther along the valley 6 rabbits were examined and found to be absolutely free from them. There were no apparent differences between the two areas, but on determining the *p*H of the soils it was found that the soil from the positive area (*p*H 7·9) was slightly more basic than that from the negative area (*p*H 7·6). However, in August both areas were swarming with harvest mites.

Many observers have commented on the localized distribution of harvest mites. This cannot be shown on a small-scale map, as it concerns areas too

Scale in miles
0 10 20 30 40 50 60 70 80 90 100
● Identified from specimens
◐ Seen by observers
○ Known from bites only
△ Believed to be absent

Fig. 1

Table 1. *Number of records of* T. autumnalis *received from each county*

County	Number of records: Identified from specimens ●	Seen by observers ◐	Known from bites ○	Believed absent △	Total number of observers
Aberdeenshire	.	.	.	1	1
Anglesey	.	1	1	.	2
Angus	.	2	3	.	5
Argyll	.	.	.	1	1
Ayrshire	.	1	.	.	1
Banff	.	.	1	1	2
Bedfordshire	.	1	2	.	3
Berkshire	2	7	5	.	14
Berwickshire	.	1	1	1	3
Buckinghamshire	.	8	6	.	14
Bute	1	.	.	.	1
Cambridgeshire	.	2	3	.	5
Cardiganshire	.	2	.	.	2
Caernarvonshire	.	1	2	.	3
Channel Islands	.	.	4	.	4
Cheshire	.	.	2	.	2
Cornwall	.	5	1	.	6
Cumberland	.	1	4	.	5
Denbighshire	.	1	1	.	2
Derbyshire	.	.	2	.	2
Devonshire	.	5	5	3	13
Dorsetshire	1	17	15	.	33
Dumbartonshire	.	.	.	3	3
Dumfriesshire	.	.	1	1	2
Durham	.	.	1	1	2
East Lothian	.	2	.	.	2
Essex	.	2	1	.	3
Fife	.	3	3	.	6
Glamorganshire		1	3	.	4
Hampshire	1	4	12	2	19
Herefordshire	.	3	3	.	6
Hertfordshire	1	4	6	.	11
Huntingdonshire	.	.	1	.	1
Inverness-shire	.	1	.	2	3
Isle of Wight	.	5	5	.	10
Kincardineshire	.	.	1	.	1
Kent	1	11	15	1	28
Lancashire	.	1	2	1	4
Leicestershire	.	1	.	.	1
Lincolnshire	.	4	5	.	9
Midlothian	.	.	1	.	1
Monmouthshire	.	.	2	.	2
Montgomeryshire	.	3	2	.	5
Moray	.	.	2	.	2
Nairn	.	.	.	1	1
Norfolk	1	1	2	.	4
Northamptonshire	.	3	3	.	6
Northumberland	.	2	11	.	13
Nottinghamshire	.	.	2	.	2
Oxfordshire	.	6	8	.	14
Perthshire	.	1	2	.	3
Ross and Cromarty	.	1	1	2	4
Roxburghshire	.	2	2	.	4
Selkirkshire	.	.	1	.	1
Shropshire	.	3	3	.	6
Somersetshire	2	8	5	.	15
Staffordshire	.	.	2	.	2
Stirlingshire	.	.	1	1	2
Suffolk	.	2	2	.	4
Surrey	.	5	9	3	17
Sussex	.	13	12	5	30
Warwickshire	.	.	3	.	3
Westmorland	.	.	.	2	2
Wigtownshire	.	1	1	.	2
Wiltshire	1	3	7	.	11
Worcestershire	1	3	.	.	4
Yorkshire	1	6	8	10	25

small to be indicated. Nevertheless, it is a characteristic feature of the distribution of the harvest mite that an infested area may adjoin a habitat similar in all respects but free from harvest mites. In the introduction reference was made to the local distribution of *T. akamushi* in Japan. This was commented on by Ashburn & Craig (1908) and again by Sambon (1928). André (1930, p. 54) quotes the observations of Toldt and Methlagl on the local distribution of *T. autumnalis* in the Alps which the authors were entirely unable to explain. Ewing (1921) has noticed a similar sporadic distribution of *T. irritans*, the American chigger, in the United States.

Vegetation does not appear to be a limiting factor. Grasslands are the most favoured haunts, but harvest mites also occur very frequently among corn and are a great source of annoyance to anyone walking through stubble in affected areas. They are also found among bracken, and many observers have found them in gardens, particularly on raspberries and beans. There are also records from woodlands.

The actual distribution of the harvest mite in the British Isles has now been to some extent determined, but the reason for that distribution remains a mystery and will probably continue to do so until the adult is found and the requirements of the nymph and adult are known.

3. Hosts

(*a*) *Summer*

T. autumnalis, so far as we know, attacks only mammals and birds. André (1930, p. 45) gives a list of animals on which harvest mites have been found on the continent. Observers in this country who answered my enquiry about harvest mites have found them on the following animals:

Dog. From 51 observers we have records of dogs being troubled by harvest mites. They form little orange clusters which can be seen on the ears, between the toes, on the legs—particularly the thighs, on the underparts of the body, on the margin of the eyelids and on the nose. Sporting dogs, particularly those which hunt rabbits, are the most severely attacked.

Rabbit (*Oryctolagus cuniculus*). In some districts wild rabbits are very badly infested with harvest mites. The records (19) are fewer than those of dogs, but as so many more people are likely to observe dogs than rabbits, the numbers are not significant. The parts of the body affected are ears –inside and outside —anus, corner of eyes, and paws. In the harvest mite "season", the rabbits are attacked all over the body, but particularly on the under surface.

Cat. Cats do not usually wander so far abroad as dogs, and therefore do not come into contact with harvest mites to so great an extent. Eighteen records have been received of cats being affected. Again the ears are most often attacked, but in addition, clusters of the mites have been seen on the tip of the tail, between the claws, on the legs, neck, top of head, on the face, near the whiskers, and on the under parts of the body.

Horse. Seven records have been received of horses being affected by harvest mites. Generally the mites are found on their faces, particularly around the nose, though sometimes around the eyes, and have obviously been picked up while the horses were feeding.

Sheep. Sheep grazing on chalk downs are liable to be attacked by harvest mites. The face is usually bitten. Three records of sheep being affected have been received.

Wood mouse (*Apodemus sylvaticus*). Around the anus.

Bank vole (*Clethrionomys glareolus britannicus*). Inside the ear.

Field vole (*Microtus agrestis hirtus*). Inside the ear.

Hedgehog (*Erinaceus europaeus*). On the face.

Shrew (*Sorex araneus castaneus*). In a previous paper (Elton & Keay, 1936) it was stated that although a large number of shrews had been examined, no harvest bugs had been found. Since then a report has been received from an observer who found a shrew very badly infested on its ears and body.

Stoat (*Mustela erminea stabilis*). Part affected not recorded.

Hare (*Lepus europaeus occidentalis*). Part affected not recorded.

Grey squirrel (*Sciurus carolinensis*). Seen in region of genital organs and anus, also in the ears and on the back.

Partridge (*Perdix perdix*). Birds which spend a great part of their time on the ground are affected by harvest mites. The parasites are not very easily seen among the feathers and must have escaped observation in many districts. Six observers have recorded their occurrence on partridges. They were found on the legs, under the wings, on top of the head and around the anus.

Pheasant (*Phasianus colchicus*). In two cases reports have been received of harvest mites found on pheasants. They were found on the legs, particularly on the thighs.

Fowl. On the legs. (Hirst (1926) obtained harvest mites from chickens.)

Turkey. Round emerging feathers of a young turkey.

Sparrow (*Passer domesticus*). Around the anus.

The choice of habitat on the host is as inexplicable as the geographical distribution. Certain habitats are favoured on different hosts. The most usual habitat is inside the ears. Harvest mites are found in the ears of dogs, rabbits, cats and voles. In other cases they are found around the anus. This is so in the wood mouse, in the rabbit occasionally, and in the sparrow. In August and September when the harvest mites are so prolific they attack other parts of the host, but are always to be found in abundance also on the originally affected parts.

(*b*) *Winter*

Free living harvest mites are found mostly in August and September. After this the numbers diminish and there are no further attacks on man until the following summer. The question arises as to whether *T. autumnalis*

passes the winter in the larval, nymphal or adult state. Comparing *T. autumnalis* with *T. fuliginosum* Toldt (André, 1930, p. 53) supposed that the mite passed through a complete life history in one year, the adult over-wintering and laying eggs which hatch in the spring. But the occurrence of larval *T. autumnalis* in November and April suggested the possibility of the larvae over-wintering. Bruyant (1909*b*) had previously stated that he had found a number of larvae in the ears of a wood-mouse in January, a finding which was in accordance with a theory of over-wintering.

In this country it has been ascertained that *T. autumnalis* larvae do over-winter in some districts. The rabbit is probably an important reservoir during the winter. The mites were found on rabbits' ears in February at Chewton Mendip, Somerset. Rabbits caught at Ilsley in December, February, March, April and May had clusters of the mites in their ears. These were for the most part very small and were only to be found in a little pocket fairly deep in the ear. 72 rabbits were examined. The numbers of harvest mites remained fairly constant throughout the winter, an average of 26 being found on each rabbit. In May the numbers decreased and were still lower in June. This was not due to the fact that young rabbits were being caught in addition to old ones, for the young rabbits were equally affected. Of two young rabbits caught early in May, one, about 4 weeks old, had 15 larvae in its ears, and the other, approximately 6 weeks old had 38 larvae in its ears. In July the numbers had increased again and in August were prolific.

A corresponding seasonal curve for the bank vole was discussed in a previous paper (Elton & Keay, 1936). The voles were trapped over a period of 3 years in Bagley Wood, near Oxford, and a large collection of harvest mites was made. The highest rate of infestation occurred in September, after which the numbers declined throughout the winter until half-way through May. After this no mites were found on the voles until the end of July, when the numbers increased rapidly, reaching the maximum in September. The wood mouse and the field vole were also trapped. Harvest mites were found on the wood mouse until December, and voles until November. They reappeared on both animals in July. These two animals were not therefore of importance as winter hosts near Oxford during the years that trapping took place. The bank vole, on the other hand, was an effective winter reservoir.

The seasonal curve for *Clethrionomys* and *Oryctolagus* suggests that the adult should be looked for in June and July. It may be only short-lived and the fresh outburst of larvae in August may be due to the hatching of eggs laid by the adults during the two previous months.

Until the adult mite is discovered it is impossible to say whether it is the exception or the rule for the larvae to change into nymphs and adults in the autumn or in June–July, but it is obvious that over-wintering of the larvae does occur in some parts of Great Britain.

4. REARING OF THE NYMPH

Only one specimen of the nymph stage of *T. autumnalis* has been reared in England, by Hirst in 1926. He obtained several hundred larvae from some live chickens and put them into little glass cells. 33 days later a single nymph was found in one of the cells.

André (1930, p. 72) succeeded in rearing 14 nymphs in 1928. He took some free larvae and put them on the ears of a young rabbit. After about 70 hours some of them had become fully fed and were walking among the hairs. These were collected and put into sterilized soil in an atmosphere saturated with moisture. The larvae immediately buried themselves and 33 days later 14 nymphs were discovered moving about actively in the soil.

Hirst was only able to describe the ventral surface of his specimen, but André has given a complete description of the animal. In my experiments a considerable number of nymphs were reared, agreeing in detail with those bred by Hirst and André. Mounted specimens of nymphs are being deposited in the British Museum.

The larvae were obtained from rabbits' ears. The rabbits were caught at West Ilsley, Berkshire. Unless the larvae are fully fed no further development takes place: therefore only those larvae which had withdrawn their mouthparts from the host of their own accord, and were wandering freely among the rabbits' hairs were collected. Normally these larvae would soon have fallen off the host and buried themselves in the ground.

It may be mentioned here that it was usual for large numbers of mites to walk off the ears when the latter became cold. If the ears were kept in tubes, the mites collected on the walls of the tubes. Many of these had not attained their full size, and, if put into rearing dishes, did not develop further.

The fully grown larvae were placed in glass dishes which contained damp silver sand or sterilized soil obtained from West Ilsley, covered with damp filter paper, the latter being an indicator of the humidity of the atmosphere. The dishes were covered with glass lids and were made airtight so as to prevent loss of moisture. It was found that during the spring, when the atmospheric temperature was not very high, the larvae took longer to nymphate, so they were put into an incubator having a temperature approximately equal to that of an average June day, i.e. 23° C. Some larvae were taken from rabbits' ears on 9 May but were not put into the incubator until 8 June. On 17 June, i.e. 39 days after the experiment was begun, 2 nymphs were observed moving about over the sand. From another set of larvae, incubated on 31 May, 3 nymphs were obtained on 21 June, i.e. 21 days later, and on the same day 3 nymphs were found in a dish put into the incubator on 3 June, i.e. 18 days later. In August, when the rabbits were heavily infested with harvest mites, many larvae were taken and put into containers. These were kept moist and left at room temperature, and in 14–21 days after the larvae had been captured

many nymphs could be seen wandering over the sand and under the filter paper. Often the larvae buried themselves close to the sides of the dish, and if little tunnels were made with a needle between the sand and the side of the vessel many nymphs were formed in these tunnels.

In rearing *T. autumnalis* nymphs there are but two main conditions to be observed for the experiments to be successful. These are (1) the larvae must be fully fed (in which case they are about three times their original size), (2) the soil must be kept moist. Nymphs cannot be bred in a dry atmosphere.

The nymphs obtained in the above experiments lived for 2 or 3 weeks, but did not undergo any further change. The Japanese investigators, Miyajima & Okumura (1917), succeeded in rearing the adults of *T. akamushi*. This mite is a great source of danger as a transmitter of the Japanese river fever, and has consequently been subject to much more intensive study than the English harvest mite. The Japanese authors state that the nymphs feed on potatoes, melons and other vegetables. When they have grown to a certain stage they enter the earth and pupate and in a few days the adult emerges. After this successful breeding experiment the authors found many nymphs and adults living freely under leaves, etc., over fine sandy mud precipitated by floods. Attempts to feed *T. autumnalis* on similar food have met with no success. The nymphs made no attempt to eat any of the food, nor to re-bury themselves in the sand. Similarly all efforts to find nymphs or adults under stones and vegetation and in the soil at Ilsley have been of no avail.

Hirst (1926) suggested that the nymph would probably be found living in the nests of small mammals which had been infested by larvae. André (1930, p. 131) states that his investigations of such habitats had proved fruitless. Negative results were also the outcome of a series of investigations of vole (*Clethrionomys*) nests from Bagley Wood, near Oxford, and of rabbits' nests from Ilsley. In the case of the rabbits' nests only "stops" were examined, and as these are scratched out early in the year this may account for the absence of nymphs. André's suggestion that the nymphs are soil dwellers seems much more probable particularly as his adult specimen was found buried in the ground.

Ewing (1925) has found the adult form of the North American chigger, *T. irritans*, and from this has bred larvae. The food in this experiment consisted of faecal pellets from springtails and one dead springtail.

5. Geographical distribution of Trombiculae parasitic on man

Harvest mites, belonging to the same genus as the English *T. autumnalis*, attack man in many parts of the world. An account of some of them is given by Warburton (1928). In Europe *T. autumnalis* itself occurs. In France, where it is commonly known as "rouget", it has a wide distribution. André (1928) states that it also occurs in Spain, Belgium, Denmark, Germany, the Alps and Italy (Lombardy). In Denmark a yearly epidemic disease called "August

Kneider" is caused by the mite (Portchinsky, 1914). Eight cases of "trombidiasis" were observed at Trier in the Eifel district of Rhenish Prussia where *T. autumnalis* has been found (Mallinckrodt-Haupt, 1929).

Ewing has given us a great deal of information concerning the chiggers (*T. irritans*) of the New World which are the equivalent of our harvest mites and have a very wide distribution in the United States. The "tlazahuate" of Mexico has long been known. It causes a kind of typhus. It was thought to be a distinct species, but is probably identical with *T. irritans* (Ewing, 1932). Mr L. W. Matters, replying to my letter in *The Times*, informs me that a "harvest mite" (not identified) known as the "bicho colorado" is widespread on the wheat and grasslands of the Argentine. Although the gauchos and peasants become relatively immune to its attacks, newcomers, particularly English people, suffer severely and sometimes become seriously ill with fever symptoms. *Trombicula* species which attack man also occur in Uruguay (Talice, 1930) and Surinam (Van Thiel, 1930).

The scrub itch-mite of North Queensland, Australia, is probably a conveyor of pseudotyphus. A similar form has been found in New Guinea and Celebes (Sambon, 1927). Hirst (1929) mentions another mite in south-east Australia which is known locally as the tea tree itch-mite, and causes a complaint known as the tea tree itch.

A harvest mite which has not been identified, but which is believed to be similar to the English form, occurs in Egypt. Information concerning this mite has been received from Mr H. A. Boys, in reply to my enquiry. It is rampant in the wheat fields when the harvest is cut in May, and bites from that month until December. It is not confined to the wheat fields, but is found on all cultivated land. Its bites cause very severe irritation.

The harvest mites in the East have received more attention than any others on account of the diseases which they transmit from rodent to man. In Japan *T. akamushi* causes a disease known as the Japanese river fever, or tsutsugamushi disease (the name means "dangerous mite disease"). In Sumatra a similar disease, pseudotyphus, is transmitted by *T. deliensis*. *T. ascutellaris* is also found attacking man in Sumatra. This mite occurs in the Malay Peninsula together with *T. akamushi*, *T. deliensis* and *T. hirsti* (Gater, 1932). *T. akamushi* is the transmitter of tsutsugamushi disease in Formosa. A form indistinguishable from the English *T. autumnalis* was found in Formosa by Miyashima & Okumura (1917).

The river fever is not confined to Japan and Formosa. It is reported also from South China, Indo-China, and Korea. The disease is caused by a virus of the *Rickettsia* type, which has been cultured from the anterior chamber of the eye of infected rabbits, and the cultures and subcultures have proved effective on rabbits and monkeys (Kawamura & Imagawa, 1931). Rodents, both experimentally and naturally infected, have an enlarged spleen, but otherwise appear healthy. Walch noticed this when studying an epidemic of pseudotyphus

among the workers in an overgrown rubber plantation in Sumatra (Walch and Keukenschrijver, 1923). How the larvae mites become infected is a matter of doubt. Some Japanese workers (Nagayo *et al.* 1918) have come to the conclusion that the virus is acquired from the adult, and that possibly the virus is in a special non-pathogenic state in the adult. Rats and mice are the usual reservoirs of the virus, but in the 1931 report from the Federated Malay States it was stated that the number of cases and fatality from tropical typhus were increasing, many cases being among a plantation-clearing group of labourers where rats were few. Squirrels in large numbers had invaded the estate from the jungle, and it was suggested that these might also act as reservoirs of the virus.

An unidentified "harvest mite" is reported from north-western Manchuria by Miss E. J. Lindgreen, in reply to my enquiry. This mite bites chiefly where there is pressure from clothing, just as the English harvest mite does. It was found in May and June.

6. Summary

1. Enquiries about the occurrence of harvest mites (*Trombicula autumnalis*) were made through several daily papers and periodicals. The replies furnished a great deal of information concerning the distribution, hosts and habitats of the mites. 424 points were mapped.

T. autumnalis occurs widely in the British Isles. Its distribution is shown in the accompanying map. The records have been classified according to whether the harvest mites were (1) identified from specimens, (2) seen by observers, (3) known from bites only, (4) believed to be absent. More records were received of harvest mites occurring on calcareous soil than on any other type. Their distribution is often sporadic. The limiting factors are unknown.

2. *T. autumnalis* larvae have been found in summer on dog, rabbit, cat, horse, sheep, wood mouse, voles, hedgehog, shrew, stoat, grey squirrel, hare, partridge, pheasant, fowl, turkey, sparrow. They tend to occupy a specific habitat on each animal. The larvae have been found over-wintering in rabbits' ears in Berkshire and Somersetshire, and in the ears of the bank vole (*Clethrionomys*) in Bagley Wood, near Oxford.

3. Nymphs have been reared from larvae. In rearing experiments two conditions must be observed: (1) the larvae must not be removed from the host until they are fully fed, (2) the soil must be kept moist.

4. A brief account is given of species of *Trombicula* parasitic on man in Europe, Egypt, America, Australia and the Far East, and of diseases of man carried by them.

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A RINGING TECHNIQUE FOR SMALL MAMMALS

By DENNIS CHITTY

(*Bureau of Animal Population, University Museum, Oxford*)

(*With* 5 *Figures in the Text*)

CONTENTS

PAGE

1. Introduction 36
2. Previous studies of small mammal movements 37
3. Technical details of a study of movements 38
   (*a*) The trap 38
   (*b*) The rings 41
   (*c*) Spacing of traps 42
   (*d*) Records 46
   (*e*) Effects of trapping 46
4. Discussion 46
   (*a*) Significance of recorded movements 46
   (*b*) Differences in activity of *Clethrionomys* and *Apodemus* . . 48
      1. The close-spaced grids 48
      2. Recaptures within the same set in the "rectangles" . 50
      3. Recaptures after an interval 50
      4. Trapping outside the "rectangles" 50
   (*c*) Variations in activity of *Apodemus* 51
      1. Seasonal 51
      2. Sexual 52
   (*d*) Interpretation of trapping figures 52
5. Summary and conclusions 53

References 53

1. Introduction

This paper gives technical details of a system of live-trapping, marking and recapturing small mammals. The methods have been evolved during studies on the long-tailed field mouse (*Apodemus sylvaticus*), and the bank vole (*Clethrionomys* (= *Evotomys*) *glareolus*) in Bagley Wood, 5 miles from the University Museum, Oxford. It has been the object of the investigation to find out the extent to which small mammals move about, and to develop a method of making population studies that will take separate account of density and activity. The possibilities of making a mammal census by live-trapping and marking has been suggested by Dice (1931).

The results already obtained are presented only in sufficient detail to explain early conclusions, developments in method to which these have led and

some of the problems now arising. The population aspect will be dealt with after further work.

The study has been carried out in the Bureau of Animal Population under Mr Charles Elton, to whom I wish to express my sincere thanks for help and encouragement. I have received a great deal of assistance from several people, but in particular from Mr G. H. Swynnerton, without whose continual co-operation this study could not have been undertaken. To St John Baptist College I am greatly indebted for permission to carry out the work on their property.

2. Previous studies of small mammal movements

These may be summarized as follows:

Those indicating a "homing instinct" (i.e. returns of mice released at a distance from place of capture)

(1) Johnson (1926): etherized and slit the ears of 18 *Peromyscus leucopus*. Returns were obtained from distances up to 200 yd. (one of 150 yd. in one night).

(2) Murie & Murie (1931): punched numbers in the ears of 176 *Peromyscus maniculatus* in 1929–30. Returns were obtained from distances up to 2 miles. 4 out of 40 returned from 1 mile.

(3) Townsend (1935): several returns of *Peromyscus leucopus* from 100 yd. (Marked by means of an ear-punch.)

Comments. (*a*) It is likely that returns from the shorter distances may be explained by the mice having a bigger home range than expected.

(*b*) As an alternative hypothesis to that of "homing instinct" the following explanation might bear examination: that chance wandering combined with a high activity serves to bring the animal into an area of fairly large size with which it is familiar.[1] Against this is the argument that some of the returned mice were too young to have become familiar with a large territory. Possibly, this might be offset by greater activity on the part of lately weaned mice — but this is pure speculation.

Those indicating the extent of natural wanderings

(4) Murie & Murie (1931): 78 records of distances up to 100 yd. moved between captures. Six records as follows: 140, 150 (3), 230, 400 yd. Also (on second recapture) a change of position of 175 yd. from place of original capture.

(5) Murie & Murie (1932): 5 *Peromyscus* retrapped after 1 year: 3 within 40 yd. of place of first capture; 1 at 100 yd. (having meanwhile returned from 2000 yd. away); and 1 at 200 yd. from point of release after transportation from 4 miles away.

(6) Townsend (1935): 5 *Peromyscus* recaptured once or twice at original position of capture in 16 traps set in squares and spaced singly at 35 ft. (traps

[1] The question is whether or not dispersion from place of release is random. The Muries have some evidence that it is chiefly in one direction—that of home.

closed for 24 hours after first release of animals). 6 out of 13 *Clethrionomys gapperi* also recovered once or twice at places of initial capture.

(7) Kalabuchov & Raevsky (1933): over 1700 small mammals (*Microtus arvalis*, *Lagurus lagurus*, *Mus musculus*, *Chilotus socialis*) marked with aluminium rings in the ears. Migrations, development of epizootics, and changes in numbers were studied (e.g. there was a 1·5 % daily predation of ringed animals by owls, polecats and foxes).

(8) Kalabuchov & Raevsky (1935): 4851 ground-squirrels were ringed through slits in the ears in 1930–2. The majority of recoveries after 1 or 2 years were within 0·5 to 1 km. of the place of capture. Young animals showed the most activity, performing 87 % of the movements of 250–1000 m. and constituting only 51 % of those recaptured at place of release.

(9) Kalabuchov & Raevsky (1936): the activity of ground-squirrels was found to be greatest among the young in their first month after dispersion from the burrows. Distances up to 2–5 km. were travelled (1·25–3·1 miles).

Those indicating differences in activity

(10) Townsend (1935): A system was evolved of denoting "wandering tendency value" through the use of 198 break-back traps covering 17/80 acre. Differences in activity were established between species, sexes, and in different habitats.

Comment. It is possible that in the basic assumption of the method, insufficient allowance is made for the size of the area off which small mammals may be caught, even in 3 days, by a large number of traps in a small area.

(11) Elton *et al.* (1931): Autumn-storing activities are suggested as possibly increasing the amount of movement and so the numbers of *Apodemus* coming in contact with the traps (Bagley Wood, 1925–8).

(12) Baker (1930): deals with the peculiarities of the sex ratio of *Apodemus* trapped in Bagley Wood. From October 1925 to April 1928, 813 males were taken to 646 females (126 : 100). Further, there was a noticeable increase in the proportion of males in the catch from February to April, and again from July to September. Possible explanations of these facts were offered: (1) that the "excess of males might be due in part to the greater activity of the male sex", and (2) that there might be seasonal differences in the activity of each sex.

Izotiv (1932) has made a study of the percentage of a small rodent population eaten by an owl in its habitat. Animals were ringed on the hind leg with aluminium rings similar to the first type tried in the present study.

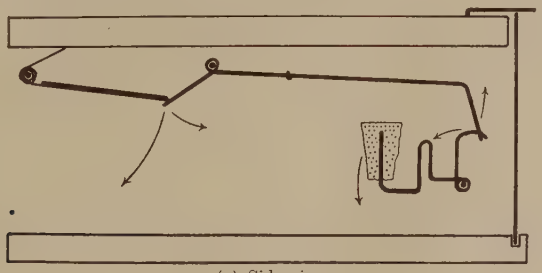
3. Technical details of a study of movements

(*a*) *The trap*

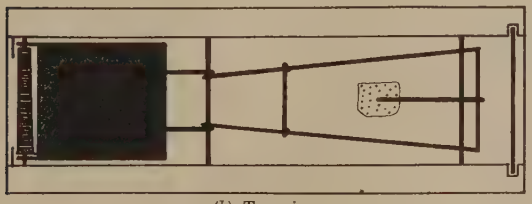
The "Tring" trap was invented in its original form by the staff of the Zoological Museum at Tring, Herts (Elton *et al.* 1931). Its cost is about 2*s*. It has since been modified in the course of long and satisfactory service at

Oxford. The form is that of an oblong box, closed at one end by a metal door and at the other by a piece of perforated zinc (Fig. 1). When the trigger (baited with coconut) is released, the door shuts, clearing the floor so that the tail of *Apodemus* is not injured. Removal of an animal is effected by taking out the perforated zinc and covering that exit with a bag into which the animal is urged by blowing through the other end.

The trap was used in this form in previous years and during the summer trapping of 1936. In cold weather deaths were frequent: e.g. between 22 and 26 October 1935, out of 26 *Clethrionomys* taken 23 died (88 %), and out of 20 *Apodemus* 7 died (35 %). However, before marking work was started, a method had been found for reducing the trap mortality. Over the end of the trap was



(*a*) Side view



(*b*) Top view

Fig. 1. The "Tring" trap. Scale: $\times \frac{1}{8}$.

fitted a $1\frac{1}{2}d.$ tin containing dry bracken for bedding and a supply of mixed grain.

In December 1935 and during the cold months of 1936 only 4 *Apodemus* have died out of 113 individuals captured and recaptured altogether 710 times. With *Clethrionomys* the death-rate has been much higher. It was possible to visit the traps only between 7 and 9 a.m., and since bank voles are active by day and night they may spend up to 24 hours in the traps. It is also possible that they learn to eat grain less readily than do long-tailed field mice, as several have been found dead without having touched the food. A more satisfactory kind of food might be found.

There is a difference in the way in which individuals of the two species react to confinement. Long-tailed field mice are always in good condition on

release. Bank voles, however, often waste energy in trying to fight their way out, and are removed dead or comatose and fouled in their excreta. In December 1935 and the cold months of 1936, out of 77 animals caught, 19 died in the traps (Table 1). 14 of these deaths occurred to unringed animals (i.e. 18 % on initial capture). Those lucky enough, or constitutionally equipped, to survive the shock of the first capture, stand a better chance of living through further nights in the traps. Deaths occurred in only 5 cases in 244 subsequent captures (2 %). Even this, however, is a death-rate per individual of 5 out of 30 (16·7 %) and combined with other factors has been a cause of considerable reduction of the population. The 23 deaths from other causes were: died in cages in the laboratory, 14; died during fitting the ring, 5; other accidents, 4. Fortunately, later methods have eliminated these last factors, though not before over half the numbers caught have succumbed for one reason or another (summer months excepted).

Table 1. *Mortality among* Clethrionomys *in all trapping and ringing operations*

Months, 1935–6	Dec.	Jan.–Feb.	Mar.–Apr.	May–Sept.	Oct. and Dec.	Total*
Unringed animals:						
Nos. caught	24	20	21	(50)	12	77
No. of deaths in traps	4	5	3	(2)	2	14
% deaths in traps	17	25	15	(4)	16	18
No. alive in traps	20	15	18	(48)	10	63
No. of deaths from other causes	4	6	7	(5)	0	17
% deaths from other causes	20	40	39	(10)	0	27
Ringed animals:						
No. liberated	16	9	11	(43)	10	46
No. not retaken	2	1	7	(39)	6	16
No. retaken in same and/or following months	14	8	4	(4)	4	30
Total no. of recaptures	114	105	19	(9)	6	244
No. of deaths in traps	3	1	1	(0)	0	5
% deaths in traps per individual	—	—	—	—	—	16·7
% deaths in traps per recapture	2·6	0·95	5·3	(0)	0	2
No. alive in the traps	—	—	—	—	—	25
No. of deaths from other causes	2	2	2	(2)	0	6
% deaths from other causes	—	—	—	—	—	24
No. of survivors (19 + 16 not retaken)	—	—	—	—	—	35
% survivors of total trapped	—	—	—	—	—	45·5

* Not including summer months.

Positions of traps are marked with 4 ft. stakes painted red and white and labelled with paraffined tags. For night work it is also necessary to mark the way to the traps by draping the trees with white cloths or newspaper, which, at a height of about 8 ft., show up well in the beam of a flashlight.

It was thought desirable to find out whether the ageing of the bait during an experiment made it less attractive after a few days. Coconut, ranging in age from 3 days to 3 months was used in lines of 25 or 26 traps parallel at 1 yd. distance from others freshly baited each day. Three such experiments were carried out in October 1935 (Table 2).

Table 2. *Animals caught with fresh and stale coconut*

Nature of bait (F. = fresh, S. = stale)	*Apodemus* F.	*Apodemus* S.	*Clethrionomys* F.	*Clethrionomys* S.	No. of trap nights
No. 1: 3–9 days old	4	10	17	12	312
No. 2: 3 months old—dry, hard	0	1	27	22	300
No. 3: 4–9 days old, dried 16 hours on radiator; covered with mould	7	6	9	6	260
	11	17	53	40	872

No. 3 bait was then used elsewhere for one night only without control line. A total catch of 64 % was composed of 7 *Apodemus* and 11 *Clethrionomys* in 28 traps.

A preference for fresh bait is suggested by the totals for *Clethrionomys*; for *Apodemus* the reverse. However, it is doubtful if either figure has any real significance. It would seem that accident or curiosity, not the attractiveness of the bait, is the reason for the animals entering the traps. The same conclusion was reached in previous work (Elton *et al.* 1931). Throughout the marking experiments fresh coconut was used at the beginning of each set and renewed only when it had been eaten.

(Townsend (1935) finds that *Peromyscus* shows little discrimination between bacon, peanut and raisin baits, but that *Clethrionomys* is mainly attracted by peanuts.)

(*b*) *The rings*

The first rings were made of zinc thin enough to be applied with the fingers of the right hand. The shape was that of an open "6" made by bending a small rectangle, 13 mm. by 3 mm., round the tips of a specially shaped pair of pliers. The ring was applied to the left leg just above the ankle, the animal being held in the left hand as follows: scruff of neck between thumb and index finger; left foot between middle and third fingers.

A few of these rings slipped over the ankle on to the foot, some came off completely and others were defaced or tightened by the teeth. Thicker zinc was tried but the rings proved too strong to be fitted in the field during cold weather, and it was necessary to take animals to the laboratory. (They were transported in cloth bags and put into small cages in which they spent as a rule 24 hours.) Numbers were stamped[1] on the rings in duplicate instead of being scratched in one place only. Also the fur of each animal was clipped in a distinctive manner, of which a drawing was made. During the summer females were marked by clipping only (see below).

By these methods there was small chance of confusion of identities; but after a few weeks some of the rings were unreadable. In May 1936 rings were made of nickel, which was of sufficient hardness to escape damage (aluminium has not yet been tried). It was difficult to fit these rings and the technique had become laborious and inefficient. There was obvious need of a ring that could

[1] The digit 1 is omitted as it makes a line of weakness across the ring.

be fitted quickly in the field, and since 1 October 1936 the following methods have proved highly successful.

These rings (Fig. 2 *a*) are made without overlap from a rectangle of $\frac{1}{2}$ mm. pure nickel foil 9 mm. × 3 mm. and are carried in the field. Before each trap is opened a ring is placed in a pair of "spring pliers" (Fig. 2 *b*). The animal is secured (as before) and the ring is applied with a single squeeze. Each is carefully inspected after it is fitted. Any that appear too tight are removed in the laboratory by means of two pairs of pliers (Fig. 2 *c*). The animal is secured meanwhile in a narrow sheath of $\frac{1}{4}$ in. mesh fish netting, through which the leg protrudes. (These removals are seldom necessary.)

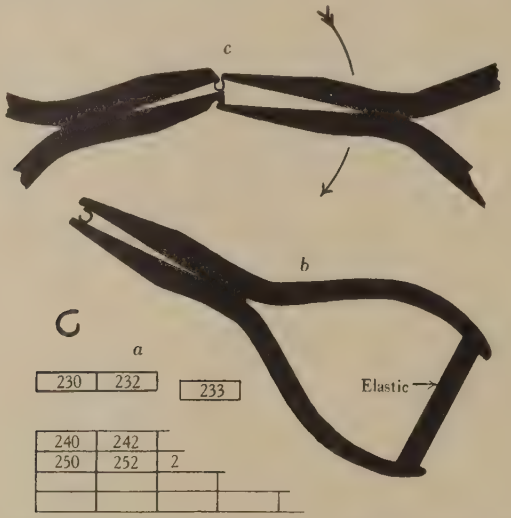


Fig. 2. (*a*) Making the rings (× 1). (*b*) Pair of "spring pliers" with ring inserted (× $\frac{1}{2}$). (*c*) Method of opening a tight ring (× $\frac{1}{2}$).

(*c*) *Spacing of traps*

In December 1935 a larch wood with an area of about 1$\frac{1}{2}$ acres was selected. This was divided into four sections, in each of which trapping was carried on for 6 days. 49 traps were set in a "grid" of 5 yd. spacing: 7 rows of 7 traps. It was planned to trap and ring the population of each section in turn. However, after trapping was completed in No. 1 section, few but ringed animals were subsequently captured.

Table 3. *New animals captured on four adjacent areas of* 65 *yd. square*

Section No. ...	1	2	3	4	
Date	29 Nov.–4 Dec.	5–10 Dec.	11–16 Dec.	17–22 Dec.	Total
Apodemus	15*	1	2*	0	18
Clethrionomys	22	0	2	0	24

* 1 death.

It was apparent that the high concentration of traps in the first section had caught animals from a great deal of surrounding territory; subsequently (e.g. Fig. 3) the same animals were nearly all retaken in whatever area was occupied by traps.

When traps were closely spaced, animals which had once been captured revisited the traps on the majority of following occasions (Table 4, December 1935, January and February 1936).

In January and February 65 traps were spaced over an area nine or ten times the size of the December grids. On 23 February, however, 5 *Apodemus* were retaken in another line at distances yet further off the area (70–190 yd.).

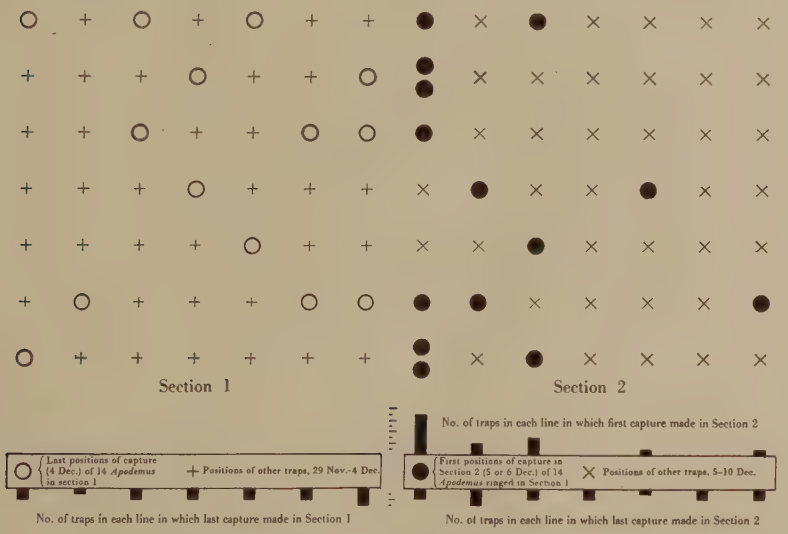

Section 1
Section 2
Last positions of capture (4 Dec.) of 14 Apodemus in section 1
Positions of other traps, 29 Nov.-4 Dec.
No. of traps in each line in which last capture made in Section 1
No. of traps in each line in which first capture made in Section 2
First positions of capture in Section 2 (5 or 6 Dec.) of 14 Apodemus ringed in Section 1
Positions of other traps, 5–10 Dec.
No. of traps in each line in which last capture made in Section 2

Fig. 3. Recapture in section 2 of 14 *Apodemus* ringed in section 1. The spacing of the traps is 5 yd.

This discovery marked a great change in outlook from the original conception of a population more or less confined to a small area. Conclusions, therefore, from the first 3 months' work were followed by several changes in method:

(1) *Apodemus* is a wide-ranging animal and *Clethrionomys* also, but to a lesser extent. *Change:* traps were spaced (*a*) *widely* not to restrict movements, and (*b*) *variously* to measure both the movements of *Apodemus* over a large area and also those of *Clethrionomys* which were expected to be more commonly below 60 yd.

(2) Continued presence of traps on an area causes localization of an otherwise diffuse population; and

(3) Animals may be continually recaught in stationary traps; the effects on the animal are unpredictable and should be minimized; normal movements

may be upset. (There is some unconfirmed evidence that *Apodemus* sometimes appears in unusual habitats after prolonged trapping.) *Changes:* the aim was now to catch each animal less frequently in each set and only after an interval had been allowed for all disturbances to subside. Traps were moved 40 or 50 yd. after each night and the number of trap nights per month was reduced.

Table 4. *Recaptures after first capture in each set*

Months 1935–6	No. of recaptures after first capture in each set	No. of times not recaught	Max. possible no. of recaptures	% Recaptures of max. possible no.	Nature of the trapping
Clethrionomys					
Dec.	77	36	113	68	3 sets: 49 traps in grid of 5 yd. spacing. (6 days each)
Jan.–Feb.	86	32	118	73	2 sets: 65 traps spaced every 10 yd. in lines 20–30 yd. apart. (7 and 10 days)
Mar.	1	17	18	6	2 sets: in "rectangles" (see text). (Figures for 4 out of 5 days only)
May–Sept.	0	37	37	0	4 sets: in "rectangles", summer system (see text)
Oct. and Dec.	2	13	15	13	2 sets: 4 days in "rectangles"
Apodemus					
Dec.	143	25	168	85	As above
Jan.–Feb.	135	14	149	91	,,
Mar.	37	21	58	64	,,
May–Sept.	26	53	79	33	,,
Oct. and Dec.	23	63	86	27	,,
Jan.	58	0	58	100	1 set in Laud's Copse: 52 traps spaced every 5 yd. in lines 10–15 yd. apart; area about 1 acre. (9 days)
Feb.	18	6	24	75	1 set in Laud's Copse: 15 traps widely spaced; moved 10–15 yd. each day. (5 days)

Since early March 1936 trapping has been carried out at fixed points in an area of some 6 8 acres. These points are grouped as shown in Fig. 4. Each group of 4 points form the corners of a rectangle of 30 yd. × 40 yd. 3 traps are put within 1 yd. of each other at each of the 9 *a* positions. After one night all are moved across the 50 yd. diagonal to *b*, and on the next two mornings to *c* and *d*. (Another system would be to trap at all positions and close the traps every other night. This was not practicable in the circumstances.) To sample the area more thoroughly an intermediate set can be run; positions *e*–*h*. During the summer each of the positions *a*–*h* was trapped for half a night at a time.

In an endeavour to discover a limit to the range of the animals, other lines of traps were run at various times. The nearest line ran completely round the "rectangles" at a distance of 80 or 90 yd. Other lines were set out at distances not exceeding 400 yd. from the nearest traps. A separate experiment was carried out in Laud's Copse on two occasions.

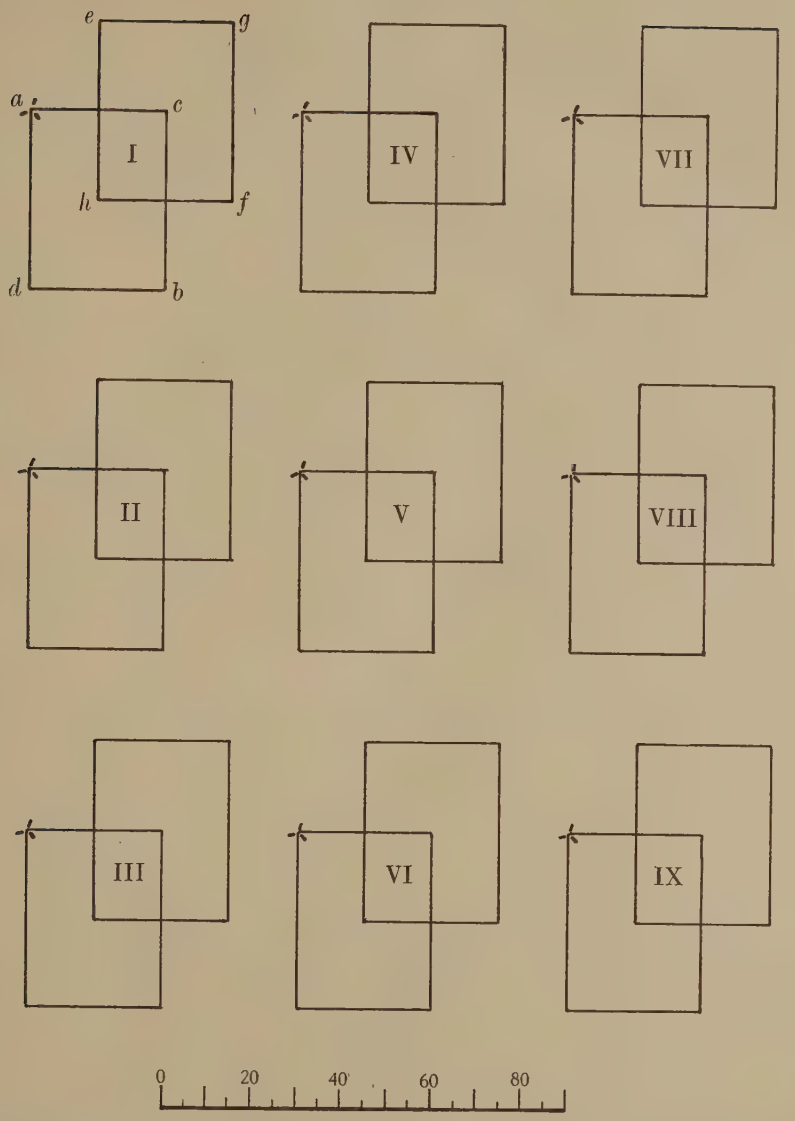


Fig. 4. The "rectangle" system of setting traps. Three traps are shown in the *a* positions. On the following mornings they are moved to *b*, *c* and *d*. Positions *e*–*h* can be used as an alternative set. (Scale in yds.)

(*d*) *Records*

Animals were weighed every time they were brought into the laboratory. At other times weights could only be estimated. A spring balance has now been adapted to field use and is proving successful. Records consist of genus, sex, weight, ring no. and trap position. These are kept separately for each animal on filing cards—white for *Apodemus*, red for *Clethrionomys*.

(*e*) *Effects of trapping*

The effects of trapping are difficult to evaluate, but the following reasons show the desirability (if natural conditions are to be maintained) of catching individuals *as infrequently as possible*:

1. (*a*) Reduced chances of meeting death from predators.
   (*b*) Unknown consequences of liberating nocturnal animals in the daytime.
   (*c*) Spread of infection through parasites, contamination of food, etc., through repeated use of trap and nesting material.

   There is no evidence about these possibilities.

2. (*a*) Unnatural concentration of animals within an area.
   (*b*) Change of habits (especially feeding).
   (*c*) Change of relative abundance of species.

   These have already been discussed.

3. (*a*) Reduced chances of meeting a mate.
   (*b*) Death of young in the nest through absence of mother.

In order to minimize interference during the breeding season, regular trapping was discontinued between April and mid-October. Instead, traps were visited after midnight and at 6 or 7 a.m. on two mornings every 4–6 weeks. It is unlikely that animals were in the traps longer than 4–6 hours. Some *Clethrionomys*, however, may have spent part of the daytime in the traps, as it was generally impossible to make an afternoon visit.

Females were released at once (after their fur had been clipped) and, in view of the mild temperatures prevailing on all occasions, it is believed that no extensive mortality was caused to the young in the nest. The height of the breeding season was passed when regular trapping was started in October.

4. Discussion

(*a*) *Significance of recorded movements*

In the present paper it will be sufficient to discuss movements in terms only of *the shortest distance between two positions at which an animal is captured either* (1) *consecutively, or* (2) *for the first time in each of two consecutive sets.* Method (2) is probably open to least objection as all captures are then made after an undisturbed interval.

Let us see what chances there are, using this second method, of recording the larger moves that an animal can make. We may imagine a hypothetical animal with a circular territory of diameter x, over all parts of which it ranges *equally and at random*. Let the relation of the traps to the territory of the animal be such as in Fig. 5. The animal may be caught in any one of the traps

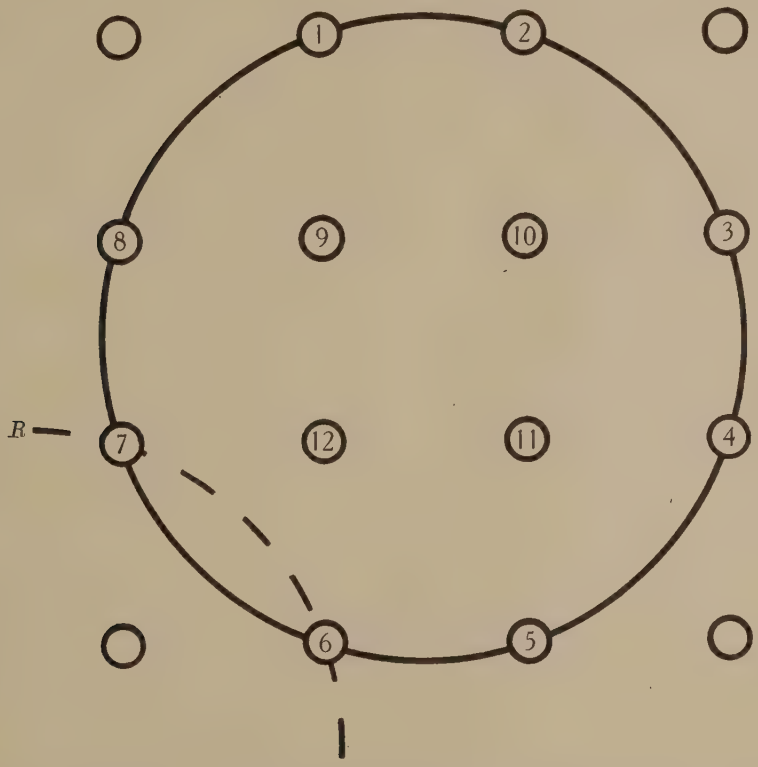


Fig. 5. Measurement of an animal's movements (hypothetical instance). The diameter of the circle is x and the distances between traps (1–12) may be expressed as fractions of x. R = range of an animal overlapping only part of the grid.

1–12 and is released at the same spot. After closure for an interval (the length of which, it is assumed, may be disregarded) the traps are reset and the mouse is again taken. When the initial position of catch is in one of the peripheral traps (1–8), the distances to each of the possible positions of second capture are those in column 1, Table 5, with the frequency given in column 3. In column 2 the possible combinations of positions are exemplified where trap 1 is the

initial position. The frequency of each distance if traps 9–12 are first occupied is given in column 5, and in column 4 an example is given, taking trap 9 as initial position.

Since there are 8 peripheral traps there are eight times as many possible combinations of positions as in column 3. Similarly there are four times as many for the central positions as given in column 5. These totals are in columns 6–8, from which follow the probabilities that a move of any one distance will be recorded (column 9). It is seen that the chances of recording any one of the three largest moves are less than those of recording any other distance. This is on the assumption of equal and random movements: but if one part of the range is more frequented than the rest, the largest distances are even less likely to be recorded.

Table 5. *Measurement of an animal's movements (hypothetical instance)*

1	2	3	4	5	6	7	8	9
	Initial position in trap 1 (similarly in traps 2–8)		Initial position in trap 9 (similarly in traps 10–12)		No. of possible combinations of positions			
Distances between traps as fraction of diameter (x) of range	Subsequent positions possible	No. of positions at each distance	Subsequent positions possible	No. of positions at each distance	Initial positions in traps 1–8	Initial positions in traps 9–12	Initial positions in traps 1–12	Probabilities of recording each distance
0·00	1	1	9	1	8	4	12	0·083
0·32	2, 9	2	1, 8, 10, 12	4	16	16	32	0·222
0·44	8, 10	2	2, 7, 11	3	16	12	28	0·194
0·64	12	1	3, 6	2	8	8	16	0·111
0·71	3, 7, 11	3	4, 5	2	24	8	32	0·222
0·89	4	1	—	—	8	—	8	0·056
0·95	6	1	—	—	8	—	8	0·056
1·00	5	1	—	—	8	—	8	0·056
	—	12	—	12	96	48	144	1·000

In the present state of knowledge it will serve no purpose to pursue further this purely abstract conception. It is obvious, however, that in any such system of measuring movements there will be a relation between the spacing of the traps and the frequency of distances recorded (with time as a probably complicating factor). It may one day be possible to establish some relationship.

The probabilities of recording movements are affected practically by the difficulty of setting sufficient traps to fill all positions simultaneously, and of ensuring that at each there will be no fewer traps than animals to occupy them. When the range of an animal overlaps only part of a grid (R, Fig. 5) no large moves will be recorded.

(*b*) *Differences in activity of* Clethrionomys *and* Apodemus

1. *The close-spaced grids.*

Movements within a close-spaced grid give no indication of the extent of natural wanderings. The following figures, however, have a few points of interest (Table 6).

Table 6. *Frequency of distances moved between closely spaced traps*

Formation of traps	Grid of 5 yd. spacing; 49 traps set 6 days in each section between 29 Nov. and 22 Dec.						Grid moved into next section			65 traps spaced every 10 yd. in lines 20–30 yd. apart			
	No. of section				Totals		No. of section into which moved			11–17 Jan.	12–21 Feb.	Jan.–Feb. totals	
Distance moved (yd.)	1	2	3	4*	No.	%	2	3	4			No.	%
Clethrionomys													
0	3	5	10	—	18	23	—	—	—	14	21	35	41
1–30	24	10	23	—	57	74	6	1	2	17	32	49	57
31–60	0	1	1	—	2	3	3	6	3	0	2	2	2
61–74	0	0	0	—	0	0	0	3	0	0	0	0	0
	27	16	34	—	77	100	9	10	5	31	55	86	100
Apodemus													
0	5	11	8	—	24	17	—	—	—	8	24	32	24
1–30	44	43	30	—	117	82	10	2	4	14	68	82	61
31–60	0	0	2	—	2	1	4	9	8	8	11	19	14
61–72	0	0	0	—	0	0	0	1	0	0	2	2	1
	49	54	40	—	143	100	14	12	12	30	105	135	100

* Not comparable—snow on last three nights.

This table calls for the following comments:

(1) *In the stationary grid of 5 yd. spacing*, movements of both species are hindered by the high concentration of traps, and distances over 30 yd. are seldom recorded. A different grouping of distances shows that *Apodemus* has the higher frequency of 21–40 yd. moves (16·1 %:7·8 %).

(2) *When traps are removed to another section*, longer journeys are performed by both species, *Clethrionomys* actually having the higher frequencies—percentages not calculated.

(3) *With wider spacing of traps*, *Apodemus* is found to travel fairly often from line to line (20 or 30 yd.) while *Clethrionomys* mainly revisits the same trap (41 % of all occasions) or wanders up and down the same line.

Table 7. *Frequency of distances moved in 1–4 days*

	Dates and system of trapping (in the "rectangles")								
	5 days *a–d* –*a*	5 days *e–h* –*e*	4 half-nights *a–h*				4 days *a–d*		
Distance moved (yd.)	10–14 Mar.	26–30 Mar.	27–28 May	23–24 June	4–5 Aug.	8–9 Sept.	20–23 Oct.	10–13 Dec.	Totals
Clethrionomys									
0	1	1	—	—	—	—	—	—	2
30	1	2	—	—	—	—	—	—	3
40	—	1	—	—	—	—	—	1	2
50	—	—	—	—	—	—	—	1	1
	2	4	—	—	—	—	—	2	8
Apodemus									
0	1	0	—	—	—	—	—	—	1
25–30	4	5	1	4	1	2	1	9	27
31–60	11	15	1	1	3	3	6	5	45
61–90	2	3	—	1	4	3	—	1	14
91–120	2	1	—	1	—	—	—	1	5
121–150	—	4*	—	1*	—	—	—	—	5
	20	28	2	8	8	8	7	16	97

* All performed in 1 day.

2. *Recaptures within the same set in the "rectangles"* (Table 7).

It is comparatively rare for *Clethrionomys* to be taken twice in the same set, even though this can be achieved by a move of 30 yd. in 2 days. Some *Apodemus*, on the other hand, may be taken every night, making minimum moves of 40 or 50 yd. (Compare also Table 4, Mar.–Dec. 1936.)

3. *Recaptures after an interval* (Table 8).

Recaptures of *Clethrionomys* indicate that, in general, this animal does not travel as widely over the area as does *Apodemus*.

Table 8. *Frequency of distances moved between first positions of capture in two consecutive sets*

	Dates of recapture										
Distance moved (yd.)	11–14 Jan.	12–16 Feb.	10–14 Mar.	26–30 Mar.	27–28 May	23–24 June	4–5 Aug.	8–9 Sept.	20–23 Oct.	10–13 Dec.	Totals
Clethrionomys											
0	0	1	0	0	0	0	1	0	0	0	2
1–30	4	5	4	3	1	1	—	1	1	1	21
31–60	4	3	3	2	1	0	—	—	1	1	15
61–63	2	—	—	1	—	1	—	—	—	—	4
	10	9	7	6	2	2	1	1	2	2	42
Apodemus											
0	0	1	0	0	0	2 (1)	0	1 (1)	0	2 (2)	6
1–30	2	4	4	6	4	2	2	2	4	0	30
31–60	6	4	6	2	0	1	1	1	0	4	25
61–90	0	1	5	5	2	0	0	3	3	1	20
91–120	1	—	3	0	1	1	0	2	—	0	8
121–150	—	—	1	2	1	1	0	—	—	2	7
151–180	—	—	—	—	1	1	1	—	—	—	3
200	—	—	—	—	—	—	—	—	—	1	1
	9	10	19	15	9	8	4	9	7	10	100

Figures in brackets indicate number of recaptures in outside traps (cf. *R*, Fig. 5).

4. *Trapping outside the "rectangles"* (Table 9).

Trapping at distances over 90 yd. from the outside traps of the "rectangles" has been of a limited and irregular nature. It therefore seems likely (1) that even the largest moves recorded are by no means the greatest that may occur, and (2) that the amount of large-scale movement is probably greater than indicated by present figures.

These data show conclusively that *Apodemus sylvaticus* makes quite large natural journeys. In many cases the distance between extreme positions of *all* captures exceeds that between two consecutive positions: e.g. *Apodemus* no. 88–600 yd. (extreme), 480 yd. (consecutive). The exact size of the home range is still a matter of speculation. It probably varies at least with the habitat and season. The Muries (1931) suggest 100 yd. as the usual diameter of the home range of *Peromyscus* trapped by them. However, it may be that the records of 140–400 yd. are representative of wider limits generally.

Table 9. *Movements outside the "rectangles"*

Ring no.	Sex	Approx. wt.* (g.)	Intervals between captures (1936)	Distance moved (yd.)	
Clethrionomys					
334	♂	16	1 Apr. –23 June	150	
E 60	♂	16	1 Dec. –22 Jan. (1937)	300	
Apodemus					
00	♀	20	21 Feb.–23 Feb.	70	
393	♀	20 ?	8 Sept. –9 Sept.	80	
			9 Sept. (1–7 a.m.)	80	
36	♂	20	21 Feb. –23 Feb.	100	
374	♂♀	21	4 Aug. –8 Sept.	100	
67	♂♀	17	20 Feb. –23 Feb.	110	
342	♂♂	24	4 Apr. –28 May	120	
25	♂♀	20	21 Feb. –23 Feb.	170	
84	♂♀	18	21 Feb. –23 Feb.	190	
374	♂♂	21	8 Sept. –9 Sept.	190	
367	♂♀	20 ?	24 June–22 Oct.	200	
	♀ (4) ♂ (9)	15 to 22	26 Mar.–4 Apr.	80 to 200	13 mice
91	♂♂	20	19 June–23 June	300	
402	♂♂	20	8 Sept. –8 Nov.	300	
86	♂♂	21	14 June–24 June	330	
342	♂♂	24	28 May –12 June	370	
86	♂♂	21	28 May –14 June	370	
91	♂♂	20	29 Mar. –19 June	460	
88	♂	18	27 May –18 June	480	

* Baker (1930) gives 15 g. as a convenient weight at and above which *Apodemus* may be regarded as adult, and 14 g. for male *Clethrionomys*.

The methods of recording movements have so far mostly supplied negative evidence of much activity on the part of *Clethrionomys glareolus*. It may be asked whether this apparent failure to make *more* long journeys may not be partly because, through the constant movement of traps, insufficient time is allowed for these journeys to be made or for the traps to be located. We know nothing of how an animal discovers a trap, and the comparative lack of data for *Clethrionomys* may be due (apart from the smaller number of surviving animals) to specific ways of searching or to psychological peculiarities. That the use of the same methods to trap different species will not give comparable results has been recognized (Dice, 1931). Present experience bears further witness to the difficulties of studying mixed populations, even though, in contrast, for example, to most North American habitats, only two species are here encountered.

Nevertheless, although the methods employed have not been well suited either to the survival or recapture of *Clethrionomys*, there is sufficient evidence that this species is much less active than is *Apodemus*.

(*c*) *Variations in activity of* Apodemus

1. *Seasonal.*

Relatively large catches in January or February were a definite feature of trapping in Bagley Wood in the years 1927 and 1928 (Elton *et al.*, 1931). It was probably significant of a general increase in activity that in February 1936

events took the form of an invasion of the trapping area in the latter part of the month (Table 10).

Table 10. *Composition of an* Apodemus *population, January and February* 1936

Date	11–17 Jan.	12–16 Feb.	17–21 Feb.
Ringed mice recaptured	9	10	12
New mice added	1	2	17
% increase	11	20	140

2. *Sexual.*

Up to the present neither the nature nor extent of these differences are quite clear. However, two points of interest are the following: (1) the largest moves have all been performed by males (Table 9); (2) of the 17 new mice that invaded the area in February (Table 10), 12 were males compared with a previous sex ratio of about equality (29 November to 16 February).

It should be noted that these preliminary observations are in agreement with the suggestions of Baker (1930), given in an earlier section of this paper.

(*d*) *Interpretation of trapping figures*

The present study shows what care must be taken in making absolute censuses to see that no animals enter or leave the area being trapped out (Dice, 1931). The exclusion of *Apodemus* from small quadrats must be a problem of some difficulty. Williams (1936) gives estimates of absolute abundance based on trapping out small areas over a period of several days. He states that the figures are rendered too high by the influx of small mammals from adjacent territory.

In making censuses of the relative numbers of different species, allowance may have to be made for the relatively greater area off which some species are trapped. Suppose, for example, equal numbers of *Apodemus* and *Clethrionomys* are taken in a given line, and that the former have wandered in from a larger area than have the latter. Then *Apodemus* will be the less numerous species, though the percentage catch is the same for both.

For comparison of catches reckoned as percentages of trap nights, the necessity for setting a standard line becomes more significant when it is realized what large-scale movements may be going on. If a limited number of animals are wandering freely over an area, the likelihood is that a small number of traps will suffice to catch the greater part of the population. A large number of traps would lower the apparent efficiency of the line.

To some of the problems here raised it is hoped that at least a partial solution will be provided by further work.

5. SUMMARY AND CONCLUSIONS

1. Through the use of a nest-box with the Tring trap, deaths of *Apodemus sylvaticus* are considerably reduced. In the case of *Clethrionomys glareolus*, several factors have contributed to a high death-rate.

2. Animals are now marked in the field with nickel rings fitted to the hind leg.

3. Stationary traps continuously set in close formation hinder diffusion of the population. It is considered undesirable that animals be retrapped too frequently.

4. Movement of a few traps over a large area gives satisfactory evidence that *Apodemus* is an active, wide-ranging species. Moves up to 480 yd. are recorded.

5. The evidence on movements of *Clethrionomys* is less complete, due to the large proportion killed and to the lower frequency of recapture. The species appears to be much less active than *Apodemus*, although one move of 150 yd. and another of 300 yd. have been recorded.

6. Variations occur seasonally in the activity of *Apodemus*, and between males and females of this species.

7. In making estimates of animal numbers, differences in activity may be a complicating factor. Determination of the true extent of the home range of each species is likely to be a problem of some magnitude.

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POPULATIONS, TERRITORIES AND BIOMASSES OF ANTS AT THORNHILL, YORKSHIRE, IN 1936

By WALTER PICKLES

(*With* 2 *Figures in the Text*)

1. Introduction

During the summer of 1935 a survey of the nests of the ants *Formica fusca* L., *Myrmica ruginodis* Nyl. and *Acanthomyops flavus* F. was made at Thornhill near Dewsbury (Yorks) (**1**). All the nests found having been disturbed for the census of the population, I undertook the present survey to investigate whether or not the ants had reorganized on the old sites or on new ones. At the suggestion of Mr C. Elton, I also weighed the ants, pupae, larvae, etc. in order to find their biomasses. The ants studied were the same species as the previous year, no new species having turned up.

I am unable to say whether the ants of any particular nest are definitely those which were there the year before as it is impossible to paint them and the only other method is by mutilation in some form. This latter idea was kindly suggested to me by Mr H. St J. K. Donisthorpe and has been used (1936) so as to be able to get if possible a more accurate movement of the ants in future.

2. Methods employed in the investigation

(*a*) *Populations*

The method used for determining populations has been the same as in my previous surveys at Thornhill and Garforth (**1**, **2**), namely, that the nests have been dug up either early in the morning or during the evening so as to bring away all the inhabitants. The inhabitants of the nests were then counted whilst still alive.

(*b*) *Weights*

In order to determine the biomass of each species, it was necessary to weigh the ants, larvae, pupae, etc., of each nest. In order to do this, I used one 250 c.c. conical (Erlenmeyer) flask for the workers, and several 100 c.c. conical flasks for the females, males and the immature forms. Before each nest was counted into the flasks, each flask was washed out, and dried, first with a cloth and finally rinsed out with acetone, the latter being allowed to evaporate away. The different sexes, and different immature forms were placed in separate flasks. The ants were not fed during the operation, the counting being done as quickly as possible. When the census of each nest was completed, the

flasks and their contents were weighed. The weight of the cleaned empty flasks was then subtracted and the weights of the contents thus found.

Of the three species under observation, *Myrmica ruginodis* was the only one which was able to live in the bare flask. The workers of this species seemed to suffer no discomfort. They gnawed at the cork which closed the flask but they did not die off. The cork was separated from the ants before weighing took place.

The other two species, *Acanthomyops flavus* and *Formica fusca* soon died when placed in empty flasks. During the process of counting they died. Few indeed managed to survive more than 2 hours or so. As such a death-rate would greatly affect my future determinations, I devised a method whereby death was completely prevented.

Into the flasks in which the adult forms were placed during the counting, a quantity of fine soil was placed. This soil had been previously sieved three times through a conical tea-strainer of fine mesh. When all the ants etc. of a nest had

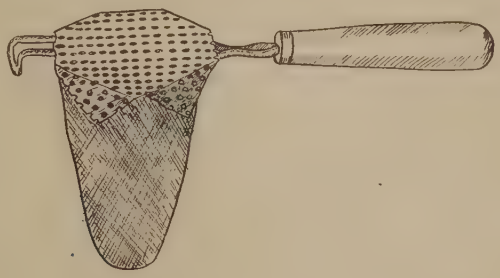

Fig. 1. Strainer fitted with loose cap made of perforated zinc, to separate the living ants etc. from soil.

been counted, portions of the soil and ants were placed in the strainer, which was then closed by a perforated zinc cap of very fine holes. The soil was then "riddled" out and as the ants were too large to pass through the mesh, they were effectively separated from the soil.

After being weighed, they were immediately returned to some soil ready for their return to the area. In this way the ants were only in the bare flask 10 min. or so, and the death-rate was thus eliminated. The larvae and pupae were cleansed of the adhering soil by being also shaken up in the strainer, the soil falling through and the cleaned larvae etc. remaining inside.

3. Recurrence of ants on the area during 1936

As mentioned in the introduction, the area was peopled again by the same species of ants as in 1935. Not all the same nests were populated, but several of last year's nests were. These latter nests were nos. 1 and 3 (*Acanthomyops flavus*); nos. 2, 6 and 13 (*Formica fusca*); and nos. 2, 5 and 8 (*Myrmica ruginodis*). Of these nests, no. 5 was last year a temporary nest, so that although the same

stone has been occupied for two consecutive years, the colony has not been continuous. As mentioned previously I hope to be more certain with regard to the movements of ants next year, having adopted the suggestion of Mr Donisthorpe.

Together with these nests, the following permanent nests have existed, nos. 17, 19 and 15 (*Formica fusca*) and nos. 8, 18 and 21 (*Myrmica ruginodis*); no new nests of *Acanthomyops flavus* have occurred. This has made a total of 12 permanent nests on the area as compared with 11 last year (1935). Of these permanent nests, several are worthy of special notice.

Nest 6 (Formica fusca)

This first occurred under the stone of 1935 and remained there until 18 July 1936. On this date, the ants had moved, and the nearest stone under which a *F. fusca* nest was found was 6 ft. away. This stone had previously not had a nest under it. I therefore concluded that the ants were those from no. 6 stone. I labelled it 6 A. During the time this nest was up for census and weighing, some more ants of the same species came and occupied the stone. This group I called 6 B. I returned both groups to the same stone and the colony flourished throughout the summer.

Nest 8 A (Myrmica ruginodis)

This nest has had a somewhat similar history to the one quoted above. During the summer, on several occasions, I have lifted the stone, and found the colony flourishing. On 3 October 1936, however, I found it had vanished; but a new colony of *M. ruginodis* had established itself under a stone, 6 ft. away. This stone had previously not been inhabited. However, when dug up and counted it contained 278 workers and 65 larvae whereas during the summer larvae and cocoons were present. I regret that a census was not taken earlier. This nest I called 8 A as I feel that they were ants from the previous nest 8.

Nest 19 (Formica fusca)

When this nest was dug out, most of the inhabitants appeared to have vanished, only 13 workers remaining under the stone on 3 October 1936. I could find no trace of the rest, but earlier in the summer the number of ants was much greater. Several of the stones, under which nests occurred in 1935, have however not been peopled this year, or else they have had temporary nests under them. These are nests 9, 11 and 12 (*F. fusca*) and nos. 10 and 14 (*M. ruginodis*).

Of the temporary nests which have been established and have vanished for some reason or other, there have been two only located, nos. 16 and 20 (*M. ruginodis*).

Actually there have been altogether 15 nests in existence: 6 of *Formica fusca*, 7 of *Myrmica ruginodis* and 2 of *Acanthomyops flavus*. These numbers

include permanent and temporary nests and their positions on the area under survey are shown in Fig. 2.

4. TERRITORIES

During the present survey I have not observed any ants to travel further away from the nest than in 1935. The maximum distances and territories have therefore remained the same as last year. These are, in the case of *F. fusca*, maximum distance 26 ft. and area of territory 2124 sq. ft.; and for *M. ruginodis*, 10·25 ft. and 330·18 sq. ft. respectively.

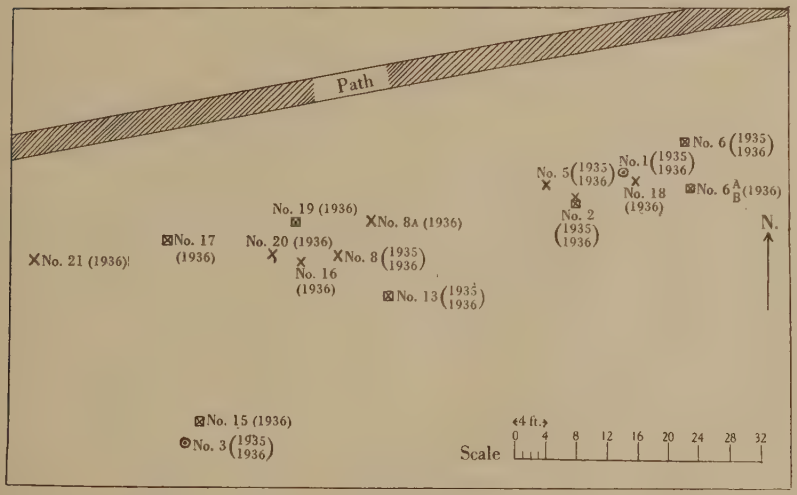

Fig. 2. Plan of the area under observation showing the positions of the nests inhabited in 1936. The dates of the nests are in brackets. × nests of *Myrmica ruginodis*; ⊙ nests of *Acanthomyops flavus*; ⊠ nests of *Formica fusca* and ⊠ mixed *Myrmica ruginodis-Formica fusca* nest.

5. POPULATIONS OF THE NESTS

The censuses of the permanent nests were carried out by digging up the nests early in the morning, so as to get the total population. By counting out the individuals, the total number both of immature forms and of the three adult castes was obtained. It is hoped that all the inhabitants of the nests were collected, as all the earth containing any ants etc. was carried away. As none of the nests were very large, the difficulty of doing this was not as great as in 1935, especially as neither nests 1 or 3 had built up the mounds of earth as they were in that year.

An analysis of the populations of each of the nests is shown in Table 1.

From this it will be seen that the nests of *Acanthomyops flavus* are more populous than those of the other two species. Apart from nest 5 (*Myrmica*

ruginodis) and nest 19 (*Formica fusca*), the nests of the latter species are on the average more populous than those of *Myrmica ruginodis*.

Table 1. *Analysis of populations of the nests*

Name of species	Date	No. of nest	Workers ☿	Females ♀	Males ♂	Larvae	Naked pupae	Cocoons	♀ pupae	Callows	Total
Acanthomyops flavus	19. ix. 36	1	1388	72	4	74	—	5	—	—	1543
	11. vii. 36	3	1722	1	—	152	—	274	61	—	2210
Formica fusca	18. vii. 36	6 A	204	1	—	3	—	124	6	—	338
	6. viii. 36	6 B	131	—	—	—	—	249	2	—	382
	7. viii. 36	17	635	28	—	—	—	85	—	18	766
	18. viii. 36	13	170	1	—	63	—	113	—	5	352
	3. x. 36	19	13	—	—	—	—	—	—	—	13
	17. x. 36	15	56	—	—	—	—	—	—	—	56
	26. viii. 36	*2	173	1	—	32	158	105	—	13	482
Myrmica ruginodis	26. viii. 36	*2	78	—	—	—	—	—	—	—	78
	20. viii. 36	5	854	23	—	84	148	—	—	50	1159
	30. viii. 36	18	451	38	—	—	—	—	—	—	489
	3. x. 36	8 A	278	—	—	65	—	—	—	—	343
	17. x. 36	21	35	—	—	—	—	—	—	—	35

* Mixed nest of *Formica fusca-Myrmica ruginodis*.

The total populations of the three species have varied from last year. In the case of *A. flavus* the population has declined. Taking *F. fusca*, the nests are on the whole more populous than previously; whilst *M. ruginodis* agrees with *A. flavus* in showing a decrease of population. Details of these populations for 1935 and 1936 are shown in Table 2.

Table 2

Name of species	No. of nest	Population in 1935	Population in 1936
Acanthomyops flavus	1	5743	1543
	3	5613	2210
	Total		
Formica fusca	6	275	720
	12	73	—
	9	218	—
	11	65	—
	13	143	352
	17	—	766
	19	—	13
	*2	249	482
	15	—	56
	Total		
Myrmica ruginodis	*2	279	78
	10	1534	—
	14	233	—
	8	660	343
	5	—	1159
	18	—	489
	21	—	35
	Total		

* Mixed nest of *Formica fusca-Myrmica ruginodis*.

As mentioned by Elton (**3**) and previously mentioned by myself (**1**, **2**), the stone covering the nest, or the mound of one, gives only a very vague idea of the population in it. Big nests have sometimes little stones and vice versa.

A list of the nests, and the size of the stone covering them, together with their populations is given in Table 3.

Table 3

No. of nest	Type	Size in sq. ft.	Population
1	Mound	0·79	1543
2	,,	1·77	560
3	Mound and stones	1·77	2210
5	Stone	0·13	1159
6	,,	0·19	720
8A	,,	0·33	343
13	,,	0·33	352
15	,,	0·23	56
17	,,	1·74	766
18	,,	0·23	489
19	,,	0·41	13
21	,,	0·20	35

6. DENSITY OF POPULATION

As suggested by Elton (**3**) and quoted by me in previous papers (**1**) and (**2**), the density of population may be expressed in three terms, the *Economic Density*, i.e. the total population divided by the territory; the *Lowest Density*, i.e. the total population divided by the area of the census; and the *Greatest Density*. This latter density is taken as the population of the nests at night. As all the nests were dug up in the early morning or evening, the total populations given may be counted as the greatest densities. *Acanthomyops flavus* does not forage for its food (**4**) and therefore this species has neither Economic nor Lowest Densities.

The densities of population are shown in Table 4. From this table we see that of the two species which forage for food, that the Economic Density of *Myrmica ruginodis* is greater than that of *Formica fusca*, while the Lowest Density of the former is also greater than that of the latter.

Table 4. *Densities of population*, 1936

Name of species	Total population*	Territory per nest	Economic density = Total population / Total territory	Lowest density = Total population / Area of census†
Acanthomyops flavus	3413	Nil	Nil	Nil
Formica fusca	1547	236 sq. yd.	1·092 per sq. yd.	1·471 per sq. yd.
Myrmica ruginodis	1956	36·7 sq. yd.	10·659 per sq. yd.	1·859 per sq. yd.

* Pupae are not included in this number.
† The area of the census is 1052 sq. yd.

As was found to be the case in 1935, there was considerable overlapping of the territories of the nests of *F. fusca*; so much so that the Economic Density is lower than the Lowest Density. The increase of the total population of *F. fusca* in 1936 has caused an increase in the Economic and Lowest Densities of this species.

7. Weights of the populations

Each of the permanent nest populations after being counted was weighed, and the analysis of these weights is given in Table 5. According to Gause (5) the biological success or failure of a species can be shown by the weights of the living creatures. These weights are as important as the actual numbers. In the case of the three species under observation, the total weights of all the living ants were:

Acanthomyops flavus = 7·037 g.
Formica fusca = 9·616 g.
Myrmica ruginodis = 3·665 g.

From these figures we see that although the total population of *A. flavus* is greater than that of *F. fusca*, the total weight of the latter is greater than that of the former. The total populations of *F. fusca* and *M. ruginodis* are approximately equal, yet the total weight of *F. fusca* nests is roughly three times as great as those of *Myrmica ruginodis*.

Judging from these facts and also that the actual numerical population has increased during 1936, it looks as if *Formica fusca* is in the ascendant.

Table 5. *Analysis of the weights of the nests (in g.)*

Name of species	No. of nest	Workers ☿	Males ♂	Females ♀	Larvae	Naked pupae	☿ cocoons	♀ cocoons	Callows	Total
Acanthomyops flavus	1	1·757	0·002	1·367	0·023	—	0·002	—	—	3·151
	3	2·133	—	0·019	0·047	—	0·841	0·846	—	3·886
Formica fusca	6 A	0·381	—	0·041	0·003	—	0·293	0·050	—	0·768
	6 B	0·395	—	—	—	—	0·985	0·050	—	1·430
	17	2·405	—	1·158	—	—	0·377	—	0·071	4·011
	13	0·508	—	0·041	0·124	—	0·644	—	0·015	1·332
	19	0·050	—	—	—	—	—	—	—	0·050
	15	0·157	—	—	—	—	—	—	—	0·157
	*2	0·691	—	0·042	0·111	0·579	0·400	—	0·045	1·868
	*2	0·148	—	—	—	—	—	—	—	0·148
Myrmica ruginodis	5	1·672	—	0·049	0·078	—	0·196	—	0·038	2·033
	18	0·763	—	0·072	—	—	—	—	—	0·835
	8 A	0·518	—	—	0·057	—	—	—	—	0·575
	21	0·074	—	—	—	—	—	—	—	0·074

* Mixed nest referred to in the text.

8. The biomasses of the species

Besides expressing the success of species as weights alone, it can also be expressed as the biomass, i.e. the total weight per unit area; in this case, since the weights are given in grams, I have chosen the square metre.

Table 6. *Biomasses*

Name of species	Total wt. in g.	Area of census in sq. m.	Wt. per sq. m. in g.
Acanthomyops flavus	7·037	880·51	0·008
Formica fusca	9·616	880·51	0·011
Myrmica ruginodis	3·665	880·51	0·004

Formica fusca again leads with the greatest weight per sq. m. (biomass) and *Myrmica ruginodis* has the least.

These figures also lend support to the statement made above, that the most successful species on this area is *F. fusca*.

9. Acknowledgements

I wish to thank Mr H. St J. K. Donisthorpe for suggestions for marking ants in the field; the Agent to the Savile Estate, Mr C. A. E. Horton for renewing permission to use the land; Mr H. Wright, Principal of the Technical College, Dewsbury, for allowing me the use of the Balance Room in the Chemical Department; and Mr Charles Elton for further help and suggestions.

10. Summary

1. A survey was made of the three species of ants living on a hill-side at Thornhill, Yorkshire in 1936, the object being to discover whether or not they had repopulated the area since the disturbance of 1935. It was found that they had done so.

2. *Territory.* The territories of the two foraging species, *Formica fusca* and *Myrmica ruginodis* were found to be the same as in 1935.

3. *Populations.* The species having the greatest population was, as in 1935, *Acanthomyops flavus*, although this had decreased in 1936. *Myrmica ruginodis* also showed a decrease in population on the previous year. Alone of the three species, *Formica fusca* showed an increase in population, although two of the nests were very small.

4. *Densities of population.* Of the two foraging species, *Formica fusca* and *Myrmica ruginodis*, the latter has a much greater Economic Density than the former; whilst the Lowest Densities of the two species are approximately the same, namely 1·4 and 1·8 (roughly) per sq. yd.

5. *Weights and biomass.* After the census of each nest had been made, the occupants were weighed and the biomass calculated. From these calculations, *Formica fusca* was found to have the greatest weight per sq. m., and *Myrmica ruginodis* the least weight per sq. m. *Formica fusca* appears to be the most successful species on the area under observation.

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THE HEATHLAND BIRDS OF SOUTH HAVEN PENINSULA, STUDLAND HEATH, DORSET[1]

By DAVID LACK and L. S. V. VENABLES

(*With* 1 *Figure in the Text*)

1. Introduction

In a previous paper Lack (**6**) published census figures for the breeding bird population of various types of British heaths and moorland, obtained as part of the programme of the British Trust for Ornithology. It was hoped subsequently to investigate the factors which affect the population density. This requires the co-operation of workers in other groups, particularly for the insects and plants. Hence the survey of animal and plant life now being organized by Diver (**2**) at South Haven Peninsula seemed to provide a unique opportunity for extending the results of the preliminary enquiry. With this end in view, the writers visited Studland in 1935 and 1936.

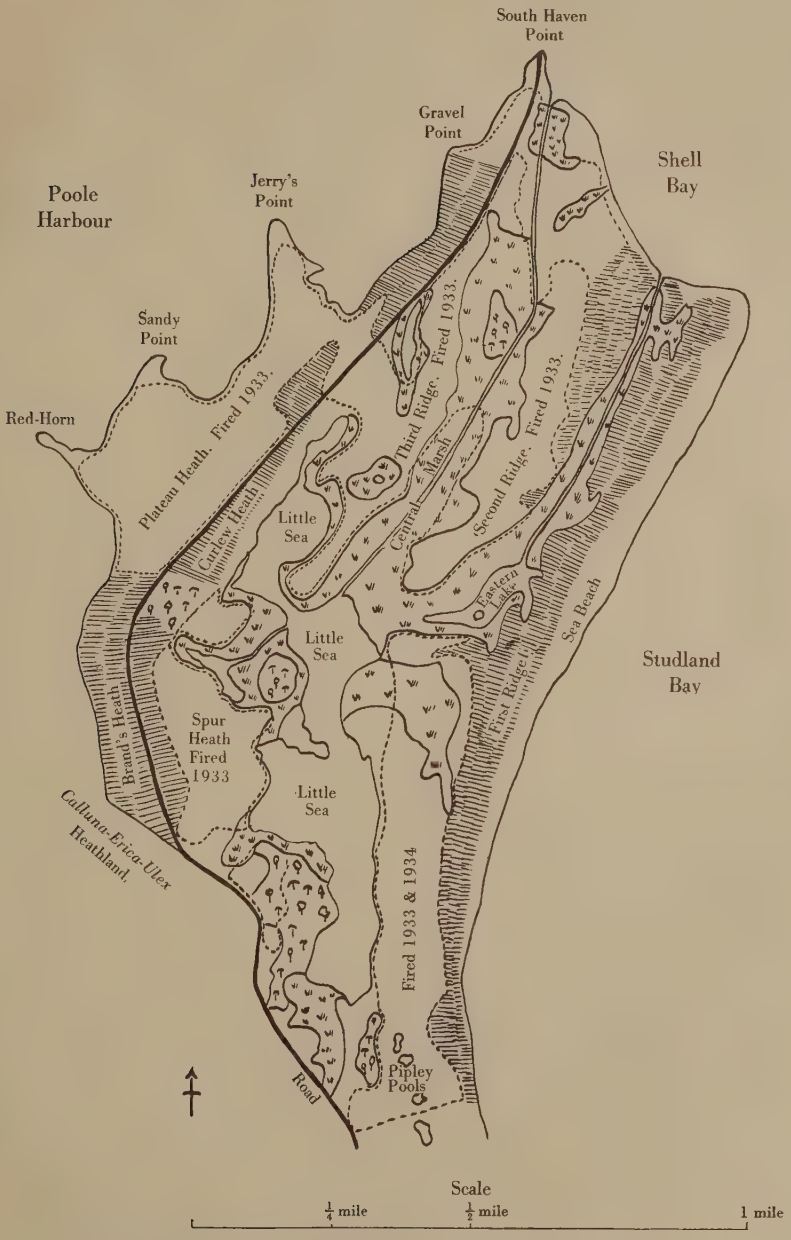
It may be said at once that we have not advanced much further in the investigation of the factors which, in a natural habitat, control the total density of the breeding population (as distinct from the factors limiting species distribution). Our main object in publishing is to provide a descriptive account of the heathland birds of South Haven, as part of the general ecological survey of the Peninsula.

During our visits we made notes on the distribution of birds other than those of the heaths. These are too incomplete to publish, and we are handing them over to Diver for the benefit of future workers.

2. Description of the areas worked

On South Haven Peninsula we investigated the heathland birds on the old western backbone and on the new eastern sands. The western backbone is composed of Bagshot beds, as is the area of heathland which we investigated south-west of South Haven Peninsula. Here *Calluna*, *Erica tetralix* and *E. cinerea* are the dominant species. We omitted the small areas dominated by *Pteris* and bushes such as *Ulex europaeus*. The eastern sands are a series of dunes of recent deposition derived from the floor of Poole Bay. Good (**3**) divides them into three main types: dune grass dominated by *Psamma*, dune heath in which *Calluna* and *Erica* are pioneers and ultimate dominants, and dry heath from which all dune species have disappeared. In our counts, the outer 77 acres of First Ridge are dune grass with a little *Calluna* and *Erica* on the inner edge;

[1] Publication of the British Trust for Ornithology. Contributions towards a Survey of the Plants and Animals of South Haven Peninsula, Studland Heath, Dorset, No. 5.



Sketch-map of South Haven Peninsula. Broken lines enclose fired areas; cross-hatch = census areas.

Second Ridge is dune heath with *Calluna* and *Erica* dominant, and comparatively little *Psamma*; Third Ridge is dry *Calluna* heath.

Unfortunately large areas of heath have been burnt recently and here there were almost no true heathland birds breeding. Our detailed census was confined to the unburnt areas.

The census areas were selected so that they should be of as uniform vegetation as possible. Any parts of markedly different character, due to bushes, fire, etc., were omitted. Hence, while the names of the census areas are those of Diver's and Good's maps, they do not necessarily refer to the whole of the area in every case. The accompanying sketch-map shows the approximate boundaries which were taken, and this, together with the fact that the size of the area worked is given in each case, should prevent confusion.

3. Procedure and methods

The breeding and winter birds of all the main areas of heath and dune on South Haven Peninsula were investigated, together with an area of heath (not marked on the map) to the south-west of the Peninsula proper and just outside Diver's survey area. The unburnt areas of heather and dune on South Haven are mainly in strips (see map), so that the total bird population could be assessed with a fair degree of accuracy by two observers travelling on a parallel zigzag course. Owing to the existence of these strips, and to the fact that the population was nowhere so dense that birds put up close together could be confused, most of the disadvantages of the "walking" method of census were avoided. (For a discussion of this and other methods see Lack (**6**).) Obviously it would have been preferable when estimating the summer population to have found each nest, and to have kept a continuous watch throughout the breeding season, but neither observer could undertake this.

For investigating the summer population we worked in the area from 27 to 30 April 1935, and from 24 to 28 April 1936, with check visits on 20 May 1935 and 22 May 1936. In the last week of April, most of the meadow pipits are in pairs and rise readily; probably almost or quite all had arrived, and extremely few had begun to sit closely on nests. Hence this time of year is the most suitable at which to estimate the breeding population. Each individual bird was marked on a map, and nearly all the areas were counted at least twice. The winter populations were counted from 19 to 21 Nov. and from 19 to 21 Dec. 1935. The method of counting was the same as in the spring counts. The south-western sample area was investigated both in summer and winter by a "rope" count; see Lack (**6**).

4. Ecological survey

The following two tables summarize the ecological distribution of the heathland birds, the first with respect to nesting sites, food and season of occurrence, the second with regard to habitat.

Table 1. *Heathland birds of South Haven Peninsula*

A. Nesting species

1. Obtaining their food (almost entirely) elsewhere:
   Shelduck, *Tadorna tadorna* (Linn.)
   Ringed plover, *Charadrius h. hiaticula* Linn.
   Lapwing, *Vanellus vanellus* (Linn.)
   Redshank, *Tringa t. totanus* (Linn.)
2. Obtaining much of their food on the heaths and much elsewhere:
   Meadow pipit, *Anthus pratensis* (Linn.)
3. Obtaining their food (almost entirely) on the heaths:
   Skylark, *Alauda a. arvensis* Linn.
   Stonechat, *Saxicola torquata hibernans* (Hart.)
   Wheatear, *Oenanthe oe. oenanthe* (Linn.)

B. Other species

1. Feeding on the heaths in the breeding season but nesting elsewhere:
   Carrion crow, *Corvus c. corone* (Linn.)
   Kestrel, *Falco t. tinnunculus* (Linn.)
   Other Birds of Prey, Hirundines, etc.
2. Regular in winter, but leaving for the breeding season:
   Dartford warbler, *Melizophilus undatus dartfordiensis* (Lath.)
   Wren, *Troglodytes t. troglodytes* (Linn.)
3. Temporary visitors in winter and on migration:
   Numerous

Table 2. *Habitat distribution of heathland birds*

Species restricted to recently fired areas

Wheatear
Ringed plover
Lapwing

Species restricted to areas of Calluna *and* Psamma

Meadow pipit
Skylark (not on South Haven Peninsula itself)
Stonechat
Dartford warbler (not recorded from *Psamma*)
Wren
Redshank

Restricted to areas with rabbit burrows

Wheatear
Shelduck

Note on the Tables.

Table 2 refers only to heathland, and in accordance with the type of occurrence given in Table 1. Some of the species mentioned occurred at the same or other seasons, in the same or other ecological niches, in other habitats on South Haven Peninsula, but our survey applies only to the heathland.

The tables do not include all the heathland species of South Haven Peninsula, only the important ones. We did not investigate the areas (rather small) dominated by *Pteris* or *Ulex europaeus*, or the isolated clumps or trees of *Pinus sylvestris*. In the *Pteris* a few red-legged partridge (*Alectoris r. rufa* (Linn.)) and pheasant (*Phasianus colchicus* Linn.) are resident. In the *Ulex*, in addition to stonechat, which also breeds on the census areas, typical scrubland species breed such as whitethroat (*Sylvia c. communis* Lath.), wren, and others. By the *Pinus*, Mr J. M. Spooner informs us, tree pipit (*Anthus t. trivialis* (Linn.)) and nightjar (*Caprimulgus e. europaeus* Linn.) breed. The last may also nest elsewhere on the heaths but had not arrived at the time of our censuses.

Nor have we included in the tables a full list of the species which feed on the heaths in summer but breed off the heaths. Carrion crow and kestrel were specified since both are regular and feed all over the heaths. Other species breeding in the woods, scrub, etc. tend to obtain some of their food from the edges of the heaths, while other species such as the sparrowhawk (*Accipiter n. nisus* (Linn.)) occasionally pay visits from outside the Peninsula. Our notes on all these species and on the numerous temporary visitors in winter and on migration have been handed to Capt. Diver.

5. Birds of the fired areas

The detailed censuses were not extended to the fired areas, but a species list was compiled for them. Most of the heath areas of South Haven seem to have suffered from fire at some time. But we refer here to those areas burnt in 1933 and later, to which the typical heathland birds have not yet fully returned. (The map shows the distribution of these areas.) Meadow pipits now breed on Plateau Heath and Third Ridge in *Calluna* patches which seem not to have suffered much from the burning. Apart from these, three species occur which are not typical of the normal heather areas.

The wheatear is regular on passage migration. In 1935 a female was seen with a newly fledged chick by a rabbit burrow on the burnt part of Third Ridge, and a breeding pair was seen near the same place in 1936. Venables (**7**) has found the wheatear to be a typical breeding species of recently fired heathland in Surrey. It disappears after the heather has become fairly thick. The wheatear is restricted to the neighbourhood of rabbit burrows, in which it places the nest; for a further discussion of this, see Lack (**5**). But this cannot account for its presence on the bare burnt areas and absence from the areas of thicker growth, for the latter contain burrows. It seems extremely unlikely that the nature of the food could be concerned, for the bird has a varied insect diet, and one would certainly have expected suitable insects to be much commoner in well-vegetated areas than on burnt ground. We have not sufficient data to determine what factor is concerned. Possibly a habitat recognition factor (see Lack (**5**)) is concerned, or possibly the food may be more readily obtained in the open.

The lapwing is also typical of the burnt areas. In 1935 and 1936 four pairs bred on the fired parts of Plateau Heath and Third Ridge. Venables (**7**) records a similar preference for burnt heathland in Surrey. The lapwing breeds occasionally on barer areas on unburnt heathland, but is absent from typical heather heath. This restriction to bare areas is not correlated with food, for at Studland the birds appeared to derive almost or quite all of their food from the neighbouring marshes. The lapwing nests in a depression on bare ground, a condition not usually supplied by typical well-grown heather heath. This would seem to be a psychological restriction, correlated with the fixity of the bird's habits. So far as one can see, it would suffer no material disadvantage if it put its nest in the heather, like the redshank, a species with very similar eggs. This point is elaborated for other species by Lack (**5**).

In 1935 one and in 1936 two pairs of ringed plover nested on the burnt part of Plateau Heath near the tidal marshes. They derived their food from the marshes. This species normally nests in a depression on shingle or other bare ground on the coast, and burnt heathland evidently satisfies its nesting requirements, while typical heather heath does not. Lack has similarly found it

nesting on burnt areas but not on heather heath on Kelling Heath, North Norfolk, about a mile from the sea.

Presumably wheatear and ringed plover, and perhaps lapwing, will disappear as breeding species from the heaths of South Haven Peninsula as the heather recaptures the burnt areas, and will return only if further areas are fired.

6. CENSUS OF HEATHLAND

The areas to which the censuses refer are delimited on the map and discussed in the description of the areas worked and in the Note on the Tables, p. 65. The breeding census included all the species of heather and marram (see Table 2) except shelduck and redshank. The shelduck bred in the rabbit burrows, and one pair of redshank nested in *Calluna* on Plateau Heath in 1935. Both species fed exclusively off the heaths, in the estuaries, etc. and neither can be considered a true heathland species, hence they are omitted. In Table 4, giving the winter census, we include only the regular species. As previously mentioned, many others occur casually.

Table 3. *Census of breeding birds*

Locality	Area in acres	Vegetation	Year	Meadow pipit *Anthus pratensis*	Meadow pipits per 100 acres	Skylark *Alauda arvensis*	Stonechat *Saxicola torquata*	Total	Adults per 100 acres
Eastern dunes									
First Ridge	77	Dune grass	1935	24	31	—	—	24	31
			1936	31	40	—	—	31	40
Second Ridge	23	Dune heath	1936	9	39	—	—	9	39
Third Ridge	15	Dry heath	1935	8	53	—	2	10	67
			1936	8	53	—	2	10	67
Bagshot areas									
Spur Heath)	19	Bagshot Heath	1935	8	42	—	2	10	53
Curlew Heath)			1936	6	32	—	2	8	42
Brand's Heath	21	Bagshot Heath	1935	10	48	—	2	12	57
			1936	6	29	—	2	8	38
Sample area west of South Haven Peninsula	41½	Bagshot Heath	1935	10	24	10	—	20	48
	34		1936	13	38	7	2	22	65

Table 4. *Census of winter birds*

Locality	Area in acres	Month in 1935	Meadow pipit *Anthus pratensis*	Meadow pipits per 100 acres	Skylark *Alauda arvensis*	Stonechat *Saxicola torquata*	Dartford warbler *Melizophilus undatus*	Wren *T. troglodytes*	Total	Adults per 100 acres
Eastern dunes										
First Ridge	77	Nov.	6	8	—	4	—	—	10	13
		Dec.	3	4	—	4	—	5	12	16
Second Ridge	23	Dec.	2 (+15)*	9	—	—	—	3	5	22
Third Ridge	12	Dec.	3	25	—	—	1	6	10	83
Bagshot areas										
Spur Heath)	19	Nov.	2	11	—	1	—	3	6	32
Curlew Heath)		Dec.	5	26	—	2	1	3	11	58
Brand's Heath	21	Nov.	—	—	—	—	2	—	2	10
		Dec.	—	—	—	—	1	3	4	19
Sample area west of South Haven Peninsula	21	Dec.	42	200	1	—	1	—	44	210

* See text.

Including only the true heathland species (as delimited above), the population of the breeding birds on the Studland heaths varied from 31 to 67 adults per 100 acres. These figures seem about average, to judge from the figures from various parts of Britain previously recorded by Lack (**6**), and include no very high or very low densities. The winter population in our counts varied from 10 to 210 adults per 100 acres. This great variation is due chiefly to the meadow pipit, under which species it is discussed.

7. Discussion of census

Meadow pipit (Anthus pratensis)

The meadow pipit is common on all of the three main habitats investigated, the dune grass, the dry heath and the Bagshot heaths. Combining the figures for the 2 years, the average density for all the South Haven areas works out at 38 adults per 100 acres. This may be compared with the main localities worked in 1934 (**6**), in which the meadow pipit densities were 5, 7, 8, 14, 19, 22, 26, 33, 37, 43, 52, 107 and 156 adults per 100 acres respectively. (These figures were not published, but can readily be obtained from the published tables.)

When the Studland populations are compared for the 2 years, First Ridge shows a fairly marked increase and the Bagshot areas a rather similar decrease. Probably one must expect such fluctuations in areas as small as those considered. Taking this variation into account, the figures show no significant difference between the breeding population on the dune grass of First Ridge and the heather areas of the Bagshot. This at first appears surprising, since the meadow pipit is insectivorous and the insect fauna of the two areas is probably markedly different. But marshes closely adjoin both areas, and here the meadow pipits obtained much of their food.

The main object of the visit to Studland had been to try to determine if a correlation exists between the breeding-bird density and the density of the food supply on the breeding grounds, particularly in view of Howard's claim (**4**) that in many species territorial fighting sets a limit which approximates to that set by food. The meadow pipit would seem to be a suitable territorial species, and is the only bird on the South Haven heaths sufficiently abundant for quantitative investigation. Unfortunately all the South Haven heaths closely adjoined to marshes where the meadow pipits obtained much of their food. Territorial fighting referred (so far as we could determine) only to the breeding grounds, as is usual in territorial species. Hence territorial spacing could have no simple correlation with food supply, any food deficiencies in the territory being readily made up in the marshes. The same fact makes any type of correlation between breeding density and food density impossible, at least in the present state of knowledge of the Studland insect fauna.

The winter density of the meadow pipits in the different areas varied between 4 and 200 adults per 100 acres. These variations are due to the fact that many, but by no means all, of the meadow pipits form into parties of 20 or

more. These parties wander, and if one is met it greatly increases the density on a small area. To eliminate this factor it would be necessary to take repeated counts throughout the winter.

The average winter density for all the South Haven heaths counted works out at 8·5 birds per 100 acres. But the marshes were not included in these counts, and a much greater proportion of pipits are found here than in summer, so that the total pipit population for the Peninsula has decreased by much less than these figures indicate. One flock of 15 birds was found on a marsh so close to the edge of Second Ridge that they might almost have been included, which would have considerably raised the total density figure.

The sample winter count of the south-western sample area gave a density of 200 adults per 100 acres. 32 of the 42 birds were in one of two flocks, either of which might have been avoided on another random count, but even excluding these the winter density is higher than that of the summer. Meadow pipits tend to move from higher to lower ground in winter, and the increase is probably due to an influx from elsewhere. The increase is curious since one would have supposed that food was much scarcer in winter than summer.

Skylark (Alauda a. arvensis)

With the meadow pipit, the skylark is the most typical British heathland bird, and it is also characteristic of *Psamma* dunes. It was therefore extremely surprising to find no skylarks breeding anywhere on the dune areas of South Haven Peninsula in 1935 or 1936; nor were they found there in winter. The skylark does occur on the Bagshot areas occasionally, one being seen in song over Brand's Heath in July 1934 (C. Diver, J. M. Spooner) and in April 1935 (K. B. Rooke), and on South Plateau Heath in July 1936 (C. Diver).

All around South Haven Peninsula the skylark is common in suitable habitats. It is much commoner than the meadow pipit on the grass-covered chalk downs a mile to the south. The Rev. F. C. R. Jourdain informs us that it was regular in the marram-covered sand dunes, now built over, at Sand Banks immediately to the north. Comparison here is no longer possible, but at our request Mr J. F. Thomas undertook a series of counts of the skylark-meadow pipit ratio on a 6-mile stretch of sand dunes with dominant *Psamma* in South Carmarthenshire. He recorded 44 skylarks and 66 meadow pipits as an average of two counts of the whole area between 3 and 11 April 1935. On all the other marram dunes in Britain with which Thomas or either of the writers is acquainted, the skylark is also regular.

On the Bagshot heaths to the west of South Haven, the skylark is almost as common as the meadow pipit, though this area is separated only by the width of the road from the Peninsula. On the south-western sample area, the average breeding density of the skylark was 24 adults per 100 acres. Comparison with the 1934 results shows this to be an average for British heathland, for which this figure varied from 0 to 44 adults per 100 acres (**6**).

The skylark is also absent from South Haven Peninsula in winter. At this season the bird tends to decrease on most heaths and sand dunes. Thus for an average of four counts (involving a walk of some 40 miles) of the Carmarthenshire sand dunes between 19 and 26 December 1935, Thomas recorded 3·25 skylarks to 29·25 meadow pipits. This is approximately 1 skylark to every 9 meadow pipits, as compared with the April ratio of 2 : 3. On the south-western sample area we recorded only 1 skylark on 21 acres, about one-fifth of the summer density; while a more extended walk gave a ratio of 4 skylarks to 50 meadow pipits. So here also the bird decreases. Nevertheless, though the skylark is generally scarcer in winter, it is clear that its typical winter density is sufficiently high for one to have expected at least a few on the 112 acres of the South Haven dunes census area. Its absence can scarcely be attributed to chance.

The dunes on South Haven Peninsula, when compared with other dunes, show an exceptionally low concentration of calcium carbonate (see Diver (**1**), discussion). They are also exceptional in that the skylark is absent. In most British dunes the outer ridge of *Psamma* is succeeded by a more or less closed turf of low plants and in some cases low scrub. But owing to the lack of calcium this phase is practically absent from the South Haven dunes. The almost pure sea-face *Psamma* is first succeeded by "dune heath", a very open community with only a few plant species among which plants of *Calluna* and *Erica cinerea* early find a place. This gives place to the almost pure carpet of *Calluna* which characterizes the "dry heath" of the oldest ridges.

As compared with this "dry heath", the heaths on the Bagshot are characterized by a much greater admixture of other species including particularly grasses, sedges, rushes and gorse. The degree of this admixture varies, becoming most pronounced on the large area of heathland to the south-west of the peninsula, where the skylark is common. Brand's, Curlew and Spur Heaths are superficially similar to and contain the same characteristic plant species as this south-western area; but Diver informs us that there are fine differences between all four heaths in the quantitative distribution of these species in the plant carpet. Brand's Heath shows the nearest approach to the conditions of the south-western area, and the skylark has occasionally been recorded here. Spur Heath, where it has not been seen, approximates more nearly to the dry heath of the eastern sands.

The absence of the skylark on the South Haven dunes would therefore seem to be correlated on the marram areas with the absence of grassy turf from the dune grass as compared with normal *Psamma* dunes, and on the heather areas with the great scarcity of grasses on the dry heath as compared with normal *Calluna* and *Erica* heath. It is interesting that in the 1934 enquiry a tendency was apparent for the skylark to be commoner than the meadow pipit on grassy heaths and the meadow pipit to be commoner than the skylark on heather heaths, the same applying also to Lack's figures for the Breckland in 1933. This is also true for Surrey Greensand heathland (see Venables (**7**)).

There is not at present sufficient evidence to determine how the skylark is affected by the scarcity of grass and turf. But it is unlikely to be *primarily* through any breeding conditions since the species is absent in the winter as well as in the breeding season. On the whole food seems the most likely factor to be concerned. The skylark feeds on both seeds and a varied insect diet, relying much more on seeds than does the meadow pipit, its usual heathland associate. Owing to the abnormal succession on the South Haven dunes, suitable seeds are scarce as compared with normal dunes and normal heather heaths. Though probably much less important, it may also be noted that the insect life of South Haven dunes is probably less abundant, and less varied (owing to the less varied plant life), than on normal dunes and heaths.

Stonechat (Saxicola torquata hibernans)

In both years, three pairs were recorded breeding on the census areas, and we recorded four more pairs breeding on other parts of South Haven Peninsula. They occurred on the heather areas, but only where there was at least one gorse bush present. The latter was an important factor in limiting distribution since heather areas without gorse were not frequented. There was one exception to this, in which a pair bred by a telegraph pole and wires. On the two winter counts we recorded 5 and 6 individuals respectively. Hence there is a decrease at this season. Most of the wintering birds were found on First Ridge, and there is no restriction to gorse or telegraph wires at this season.

The factor restricting the breeding stonechats to a gorse bush or telegraph wire would seem to be psychological, correlated with the territorial habit, for the defence of the territory involves a song and look-out post. The bird obtains its food from the ground, and occasionally on the wing, and though it at times seems to use its territorial perch as a look-out for food, this would appear to be unimportant, particularly as it can dispense with it entirely in winter. Nor is the gorse bush correlated with the nest, since the nest is placed in heather, not in the gorse bush (or, of course, on the telegraph pole or wires). Observation shows that the gorse bush is used primarily in connexion with territory and song, and it is extremely difficult to see what other requirement is met by both a gorse bush and a telegraph wire. A similar case is recorded for the tree pipit by Lack (**5**). Owing to this psychological restriction, the stonechat is nowhere near its food maximum on South Haven Peninsula, since many heather areas suitable for nesting sites and feeding are untenanted.

Wren (Troglodytes t. troglodytes)

This species is regular on most of the census areas in winter, but does not occur there in the breeding season, though it breeds in the scrub and woods of the Peninsula. The census areas do not supply its typical nesting sites, and the absence of these, and perhaps other breeding requirements, presumably account for its disappearance from the heaths in summer.

Dartford warbler (Melizophilus undatus dartfordiensis)

This bird was regular during the winter, usually in the thickest heather. We did not find it breeding on the census areas. In April 1931 Venables found a nest on Plateau Heath, in the end of a low furze spray below the surface of the heather. This area has now been fired, but some suitable nesting sites exist in other parts of the Peninsula, where it perhaps breeds, as it does on neighbouring heaths.

8. Summary

1. Tables 1 and 2 summarize the ecological distribution of the heathland birds of South Haven Peninsula.

2. The absence of the skylark from the *Psamma*, and also from the *Calluna* and *Erica* associations of the dunes of South Haven Peninsula is remarkable, since the bird is typical of these associations elsewhere in Britain. Its absence is thought to be correlated with the non-calcareous nature of the dunes, which results in an abnormal plant succession from which grasses and turf are almost absent, probably affecting the skylark primarily through its seed food.

3. In the breeding season, but not the non-breeding season, the stonechat is restricted to areas including gorse (in one case a telegraph wire). This cannot be explained through food or nesting sites, and seems correlated with the territorial habit.

4. Tables 3 and 4 summarize the census results. The breeding population varied from 31 to 67 adults per 100 acres; the winter population from 10 to 210 adults per 100 acres.

5. The breeding density of the meadow pipit varied from 24 to 53 adults per 100 acres. Its density could not be correlated with the food supply of the heaths, since the birds obtained much food from the neighbouring marshes.

6. The breeding density of the stonechat (the only other regular breeding species) could not be correlated with food supply, since, owing to its restriction to gorse bushes, it is nowhere near its food maximum.

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Phot. 1. Typical "mixed" Surrey Greensand heath. Immediate foreground: closed stand of *Calluna* and *Erica*; some *Betula* bushes. Middle hill: *Calluna* and *Erica* not yet closed up; especially retarded by exposure on hill top. Far hill: mostly *Pteridium*; various stages of both *Pinus* and *Betula* "parkland".

Phot. 2. Phase I Surrey Greensand heath. Rapid recovery of *Molinia coerulea* spreading out from ditch sides and damp patches. Bare ground with thin carpet of *Calluna-Erica* seedlings. Undamaged *Pinus* "parkland" in background.

BIRD DISTRIBUTION ON SURREY GREENSAND HEATHS: THE AVIFAUNAL-BOTANICAL CORRELATION

By L. S. V. VENABLES

(*With Plates* 2 *and* 3 *and* 2 *Maps in the Text*)

CONTENTS

		PAGE
1.	Introduction	73
2.	The ecological succession of Surrey Greensand heaths	73
3.	General discussion on the bird distribution	75
4.	Analyses of breeding territories	79
5.	Concluding remarks	84
6.	Summary	84

1. Introduction

Owing to the recent publication of various papers dealing with British heathland birds (Lack, 1933; Lack & Lockley, 1935; Lack & Venables, 1937), it has been suggested to the writer that this is a suitable time for him to record his observations on the limiting factors of the distribution of the various species typical of the breeding-bird community on Surrey Greensand heaths.

This short communication, therefore, is being made as an addition to the series, and the points brought forward in the preceding papers should be borne in mind when this one is being read. Also, the writer wishes to make it clear that he is dealing with distributional factors on one series of environments only—namely, Surrey Greensand heaths—and *not* with the general distribution of the birds under discussion over the whole of their respective ranges.

The Latin names of the birds mentioned in the text will be found under the analyses of breeding territories, pp. 80–81.

2. The ecological succession of Surrey Greensand heaths

South of the chalk ridge known as the Hog's Back, south-west Surrey, and the adjoining country over the Hampshire and Sussex borders is remarkable for the large extent of heather and pine-clad heathland. Relics of old glacial flood-plains and, later, water denudations before the great river capture by the River Wey, a tributary of the Thames, have carved out this expanse into an imposing array of ranges of hills with deep valleys between; and the heaths undulate, frequently very sharply, between 200 and 900 ft. above sea-level.

Pine woods and, to a lesser extent, small swamps are numerous, but for the purpose of the present discussion only the dry and semi-dry heathland will be dealt with.

The most important factor influencing bird distribution, and indeed the actual species make-up of the breeding community, is the particular phase which any given piece of heath has reached in the botanical succession following (usually) a fire. These phases may be roughly summed up as follows: (1) bare earth; (2) sparse carpet of *Calluna* and *Erica* seedlings (or new growth from roots if the latter have not been destroyed), moss or *Ulex nanus*; (3) half-grown *Calluna* and *Erica* bushes, rapidly closing up; (4) full-grown *Calluna* and *Erica* (18 in. to 2 ft.)—usually the last phase, see below; (5) *Betula* phase; (6) *Pinus* phase. The last is the logical climax but it is seldom reached.

Fritsch (1927) has dealt so fully with the general succession on one heath that it will be necessary here for only the briefest discussion on the six main phases of all the Surrey Greensand heaths that have come under the present writer's notice.

(1) A whole moor, completely bare, is never in the writer's experience seen after the first spring following the fire.

(2) If, as usually happens, the fire was over a well-grown high and dry stand of *Calluna* and *Erica*, then the roots are mostly destroyed. In such cases, the ground during the next few springs will show a good deal of bare earth with patches, frequently large, of such growths as *Polytrichum juniperinum*, *Rumex acetosella* and, if present before, prostrate bushes of *Ulex nanus*. The rapidly recovering *Molinia coerulea* and *Pteridium* will seize the chance of spreading from existing colonies; those of the former being usually along the sides of ditches. Practically no heather[1] seedlings will appear until the second year; and then but sparsely. If, however, at the time of the fire, the *Calluna-Erica* phase was still low and green, then the correspondingly less intensity of the fire will not kill the roots, and the recovery is rapid—a fair carpet appearing in the following spring.

(3) The *Calluna* and *Erica* bushes are well grown and are at their best for the richness of their flowers but have not yet joined up in a closed stand. *Polytrichum juniperinum* and *Rumex acetosella* have, to all practical purposes, disappeared but *Ulex nanus* is conspicuous between the heather. *Molinia* is rapidly being driven back to the ditch sides and damp patches, while the straggling explorers from the *Pteridium* patches are being crowded out.

(4) *Calluna-Erica* phase. At least 8 years have to elapse before this reaches its final 18 in. to 2 ft. height. Longer is needed should the growth be retarded through, e.g. exposure on a hill top. This, usually, is as far as the ecological succession progresses; the dry closed stand being so prevalent to fire. *Molinia* and *Pteridium* have, after all, captured little or no new ground. *Ulex nanus* and

[1] For the sake of brevity, the term "heather" includes *Calluna*, *Erica cinerea* and *E. tetralix*. The last, however, is usually only in the damper places.

Phot. 4. *Pinus* and *Betula* "scrubland"; *Calluna-Erica* phase being driven out.

Phot 3. Phase IV of Surrey Greensand heath. Showing recovery of *Calluna-Erica* and *Betula*, eight years after fire.

Cladonia are plentiful in places, but all below the heather canopy. Scattered bushes of *Ulex europaeus* stand well up.

(5) So far, no mention has been made of the birch trees (*Betula*). Actually these are irregularly distributed on the heaths and before the reintroduction of the pine, presumably formed the logical climax. However, fires during Phase 4, grazing cattle and so on, are so numerous that comparatively few birches reach the dignity of "trees".

(6) Since the local *Pinus* reintroduction during the seventeenth and eighteenth centuries, a closed pine wood is now the logical climax. Fires, however, are even more deadly to this tree than to *Betula*; for the latter will send out a circle of sturdy green shoots round the base of its fire-killed trunk in the following spring (or even during the same summer). A pine sapling does not recover if once badly burnt, and even a well-grown tree will be killed if the fire is intensified by a surrounding thicket of saplings, sprung from its own dropped cones. Many thousands of acres of Surrey Greensand heaths have been planted with pines but already most have been burnt, and it is doubtful whether the pine woods will extend their present domain by any appreciable extent until better fire-control methods are organized. Practically never does a heath last many summers at Phase 4 before it goes up in flames—significantly enough usually during a week-end or on a public holiday. Most of the pine and birch woods came into existence before the era of the omnibus and the mass-production automobile.

3. General discussion on the bird distribution

The general facts of habitat selection with particular reference to the psychological aspect have already been dealt with by Lack (1933). Again, therefore, nothing but the briefest discussion, appropriate to the local conditions, need be embarked upon here. Such further detail as is necessary will be given below. Several points, however, may be conveniently brought forward here.

Grass. Grass is frequently dominant on some recently fired heaths and is also usually a codominant on the damper ones. Its presence or absence plays its part in the distribution of some of the birds. As grass replaces heather, so do whinchats tend to replace stonechats and skylarks to replace meadow pipits. With these last two, both common species with very conspicuous songs, the effect is most striking. Sample counts are appended (p. 76).

This is probably due in part to the denseness of the growth, for the skylark will nest on a heath a few years after a fire when the heather is patchy and sparse and, when away from heathland, on waste ground or even newly ploughed fields. In other places, the writer has found the skylark well distributed on some of the poorer stony moors of Shetland with an open heather formation, and the meadow pipit breeding in some numbers among the thick,

coarse grass of Otmoor near Oxford (though it was very uncommon on the lush water-meadows nearer the Thames).

Table 1. *South-west Surrey Greensand heaths*

Heather-grass, meadow pipit-skylark comparison table

Vegetation	Method	Date	Skylarks pairs	Meadow pipits pairs
All heather	1 mile walked	May 3	.	2
All heather	1 mile walked	May 24	.	3
Heather with a little grass	100 acre census	May 4–9	1	7
Heather with a little grass	100 acre census	May 2–7	1	8
Two-thirds heather, one-third grass	1 mile walked	May 3	4	7
Half heather, half grass	1 mile walked	May 3	5	4
All grass (South Downs)	40 acre census	May 13	9	1

Lack (1933) writes of Norfolk: "The meadow pipit, common on every other heath, was absent from the bare rabbit-grazed Little Heath where its usual associate, the Skylark, remained common. Nesting requirements perhaps explain this, the former selecting rather thick ground vegetation, the latter much more open ground." Surrey heaths with dominant or codominant grass are generally a good deal more patchy than those with a pure stand of heather. See also the discussion by Lack & Venables (1937).

Ecoclimate. A distributional factor which has not so far been studied on these heaths is local variation in temperature; a subject which has been fully discussed, though from the view-point of Equatorial Africa, by Moreau (1934, 1935). The only paper seen by the writer which covers this problem at all for Europe, is one by Geiger (1927), which is devoted to agricultural land in Germany. As regards heat, he shows that erect grasses at their tops are hardly warmer by day than the open air, but the air temperature rises rapidly as the ground is approached and is as much as 4° C. more at the roots. He also demonstrates the existence of "frost hollows" which, although they may be almost invisible to the eye, seem to collect cold air and may show a difference of 10° C. on a still, clear night.

These dry sandy heaths with their dead lower branches of heather undoubtedly make for great heat which has to be endured by late ground-nesting species during a hot summer on all but the slopes facing north; while frost hollows may well influence the distribution of the earlier spring nesting birds. Apart from the obvious fact that the cold would greatly reduce the number of active insects within easy reach of the nest, and that in these hollows, getting more than their fair share of moisture, the damp-loving *Erica tetralix* and *Drosera* become codominants with a possible influence on the insect fauna; there is the direct effect of the cold upon the nestlings to be considered.

Eliot Howard (1935) has stated the following facts: that if the young are exposed to the atmosphere when the temperature falls to 50° F. they collapse quickly during the first 2 days after hatching: that there is a rise and drop of several degrees in the body temperature of the young bird when the adult is brooding and absent: that the temperature of the young varies consistently with that of the atmosphere during the first few days: and that a high rate of development can only take place when the temperature is at the optimum.

A heathland research carried out on ecoclimatic lines might well show extremes of temperature influencing the distribution of the ground-nesting species—more especially the early ones.

Trees. A very obvious factor on the choice of spring habitat for many heathland birds is the presence or absence of trees; both for use as nesting places and as song posts. The tree nesters are carrion crow, hobby and kestrel, and there is an interrelation between these as the hobby and kestrel use old crows' nests. The stock dove, too, is a tree nester on occasions, breeding in a hole, in the cup of a well-concealed fork, or in a sort of "witch's broom" (probably caused by a fungus) in the crown of a Scots pine. But as it also utilizes rabbits' or old sand martins' holes it is in no way dependent on trees.

The song post question, however, influences the majority of the birds, though with many it need not necessarily be a tree, for a bush or even a fence will do. The tree pipit must have a tall sóng post but the meadow pipit uses only a small one and readily dispenses with it if there is not one present, and in no way avoids a treeless or bushless heath. Nevertheless if a meadow pipit does own a song post it is jealously guarded, and should another male perch on it, attack instantly follows although the trespassing male (provided he does not sing) may visit and feed on other parts of the territory that are reasonably remote from the nest.

For the woodlark a song post is essential, though anything from a tall tree to a fence suffices; but the skylark very seldom uses one at all, and then it is merely a small bush and, as with the meadow pipit, the full song is not uttered. As all these four species sing regularly on the wing and two can do without song posts entirely, this is a curious point. The old *cliché* that explains a bird's choice of nesting territory by the presence or absence of food, nesting site, and nesting material, ignores what would seem to be an equally pertinent element: namely that birds are often driven by some force, which to us is inexplicable, to choose certain features.

The tree pipit is unable to get on without a high conspicuous post for use during its song flight, whereas the meadow pipit will only occasionally make use of one; and then not *necessarily* tall, as the vast majority show. While this may have started (as also with the woodlark and skylark for example) by the species' individual whims, it has now, in the case of the former, progressed so far as to be an absolute necessity. The bird seems incapable of selecting a

territory for reproduction unless a tree is present for use at the start and finish of the song flight.

The nightjar by no means infrequently sings from the ground but requires a song post for a part, at least, of his evening singing; and one bird, whose triangular territory had trees down two sides, had his courtship activity area extended by one-third when a 5 ft. pole was erected half-way along the hypotenuse. He altered his programme and used this pole regularly; as did a meadow pipit who abandoned his 2 ft. song and look-out post for a 4 ft. stick, placed a yard away.

Artificial song posts would certainly change the species make-up of the breeding bird community on a treeless heath. Lack & Venables (1937) and Lack (1933) record a stonechat and a tree pipit being confined to the parts of two heaths with telegraph poles. Most of these particular heaths were suitable for nests but natural song posts were absent.

The wheatear must have a class to himself, for he sings anywhere. Should a tall tree be growing on his territory, he sometimes sings from its branches or does song flights from the top. Should a bush be present, he does the same thing there; but should there be nothing (as is often the case owing to his frequent choice of newly fired heath), he sings from the bare ground, from a stone or mound, or becomes a remarkably poor emulator of the skylark. His song is a simple one containing a good deal of mimicry, and is not uttered as often as with most birds, so possibly it is not emotionally important and no rigid song routine has been evolved. His conspicuous plumage would "assert" him without any elaborate song.

Bushes. Other than when used as song posts, bushes (mostly *Ulex europaeus*), when they have had time to grow after a fire, are an obvious influence on the distribution of such birds as linnets, chaffinches, long-tailed tits and red-backed shrikes, which actually nest in them. Yellow and reed buntings, however, make an interesting comparison with these birds for although, like them, they nest in bushes (though generally lower down), they nest just as frequently in the heather and use the bush (or any elevated plant in the case of the latter) as a song post only.

Dampness and water. The whinchat (if there is a song post) and the skylark will breed on a damp heath apparently owing to the codominant grass and consequent patchy vegetation (see above). The grasshopper warbler, reed bunting, curlew, snipe and redshank will nest sometimes on dry heaths and sometimes on very damp ones. Even when nesting on the dry heaths, the last four birds seem, however, loth to be too far from marsh or water which is easily explicable with the curlew, snipe and redshank owing to their method of feeding—to the niche they fill, in point of fact—but it is by no means so obvious with the reed bunting.

In commenting on this sort of idiosyncrasy, Lack (1933) says: "Hereditary instinct controls the design of the bird's nest, the materials used, and the site

adopted, each species adhering to its own particular type, though the differences between closely related species cannot be explained teleologically. When instinct controls such matters, it would indeed be surprising if it did not control the type of ground selected by the bird for a breeding territory."

It is very exceptional to find heather-nesting wild duck (mallard) or teal more than a third of a mile from water but here an explanation presents itself in that the shorter the journey, the better it is for the female, and later for the newly hatched young. The actual proximity of water to small heathland-breeding Passerines seems unimportant. If there is a pond or stream not too far away from the nest, the birds will frequently leave their territories and fly to it. In many cases the territories are at least a mile from water and almost certainly the birds do not visit it while they have an occupied nest.

Food. Food preference as an influence on distribution has already been fully discussed by Lack (1933, pp. 250–1) and the data there brought forward point to it having little or no importance. With an insectivorous bird, for example, apparently almost any palatable insect will do: those coming most readily to hand being eaten.[1]

4. Analyses of breeding territories

It has been the writer's practice to analyse many individual territories of these heathland birds. When the results are examined it becomes evident that every individual species has one or several of various features in its series of territories and that these limiting factors are, to all intents and purposes, constant.

The basis of the problem is the recovery of the heath after burning, with the consequent changes in vegetation; but it is most deceptive to record this in tabular form without an extra column devoted to limitations. As an example: Phase 1 (bare earth after fire) is the most simple of the environments, and the birds usually found breeding on it are lapwing, wheatear, nightjar and woodlark. Yet (in the writer's experience) the lapwing is never far from damp ground or water; the wheatear must have a hole for its nesting-site; the female nightjar usually has some dead bracken or a tree stump under which to lie, and the male always has a song post; and the woodlark must have some ground vegetation, usually the rapidly recovering *Pteridium* (dead) or *Molinia* under which to conceal its nest, and a song post, and possibly it avoids frost hollows, being so early a breeder. Each phase becomes progressively more complicated.

Nevertheless, such points as negative evidence, the number of cases upon which the writer bases his argument, and so on, stand out so clearly in tabular form, that this has been attempted. Some slight explanations of the table must, however, first be given.

First, as to the method of analysing the territory. This is done by the nest position (the approximate position of which can rapidly be ascertained by the birds' activities, even if it is not actually found), and the *general* environment

[1] For a possible influence on the skylark, however, see **Lack & Venables** (1937, pp. 69–71).

Table 2.

For accurate *comparative* figures, the numbers should be treated horizontally, not vertically.

Species	Number of territories analysed	Phase 1	Phase 2	Phase 3	Phase 4	Limitations and common factors
Carrion crow (*Corvus c. corone*)	8	1	2	2	3	*Strong tree* (therefore usually *Pinus*) for holding the nest. Either a heathland wood or open park land will be used
Chaffinch (*Fringilla c. coelebs*)	4	.	.	.	4	*Bush* (therefore usually *Ulex europaeus* or hawthorn) for containing the nest and for use as a song post. Occasionally a tree will be used for the latter purpose and, if reasonably dense, for the former also
Linnet (*Acanthis c. cannabina*)	17			.	17	*Bush* as above. Occasionally a nest is built below the surface of the heather on the lowest branches of a *Pinus* sapling
Yellow bunting (*Emberiza c. citrinella*)	14	.	.		14	*Tree or bush* for song post. Frequently the nest is placed in the latter, but it is the song post situation and not the nesting site situation that affects the limitation. Nests are as frequently built in the ground vegetation
Reed bunting (*Emberiza s. schoeniclus*)	11		.	.	11	*Thick ground vegetation* (wet or dry) for nest. Any elevated plant will suffice as a song post; e.g. a heather spray in a dry territory or a rush in a damp one. *Proximity to a damp patch* seems essential: 300 yd. is the maximum, usually it is a matter of a few feet.
Skylark (*Alauda a. arvensis*)	33	.	2	19	12	*Sparse or patchy ground vegetation.* Most frequently Phase 3, or Phase 4 with codominant grass
Woodlark (*Lullula a. arborea*)	19	5	9	5	.	*Song post.* The nesting ground most frequently chosen is either recently fired with some dead bracken leaves or the rapidly recovering *Molinia*; or the sparse and patchy growth of Phases 2 and 3
Tree pipit (*Anthus t. trivialis*)	57	.	.	(11) 17	29	*Tree* for song post; 15 ft. high is the minimum. Poor ground vegetation —e.g. dead bracken or rough grass—will suffice for the nesting site; a marked contrast with the next species. The writer has seen tree pipits breeding freely, so long as song posts are present, all over transitional Phase 2–3 heath; but meadow pipits did not come in for several years afterwards
Meadow pipit (*Anthus pratensis*)	86	.	.	.	86	*Close stand of well-grown heather* for nest
Long-tailed tit (*Aegithalos caudatus roseus*)	3	.	.	.	3	*Plentiful bushes* for nest (usually *Ulex europaeus*) and feeding excursions
Red-backed shrike (*Lanius c. collurio*)	6	.	.	.	6	*Bush*, often rose or hawthorn, for nest and look-out post. If a tree is present, it is frequently used for the latter purpose
Whitethroat (*Sylvia c. communis*)	15	.	.	.	15	*Bush or small tree* for song post. *Thick ground vegetation* for nest. The bush is rarely used for the latter purpose on a heather moor
Dartford warbler (*Melizophilus undatus dartfordiensis*)	80	.	.	.	80	*Thick, tall heather*, minimum of 8 years after a fire. Firm support for nest below the surface of the vegetation. Either a *Calluna* fork will be used, the top of a spray of *Ulex nanus*, or the lowest branches of a *Ulex europaeus* bush or *Pinus* sapling
Grasshopper warbler (*Locustella n. naevia*)	11	.	.	2	9	*Thick growth of grass or heather* for nest: damp or dry. Occasionally a rapid *Molinia* invasion on Phase 3 will be used
Willow warbler (*Phylloscopus t. trochilus*)	14	.	.	4	10	*Tree or tall bush* for song post. Thick or moderately thick ground vegetation for nest
Stonechat (*Saxicola torquata hibernans*)	28	.	.	.	28	*Well-grown dense heather* for nest. *Bush or small tree* for song post

Species	Number of territories analysed	Phase 1	Phase 2	Phase 3	Phase 4	Limitations and common factors
Whinchat (*Saxicola r. rubetra*)	7	.	.	.	7	*Well-grown dominant or codominant grass* for nest. *Bush or small tree* for song post
Wheatear (*Oenanthe oe. oenanthe*)	17	9	6	2	.	*Hole* for nest and *sparse or absent vegetation*
Cuckoo (*Cuculus c. canorus*)	12	.	.	3	9	*Plentiful nests of small Passerines*, and tall look-out post
Nightjar (*Caprimulgus e. europaeus*)	38	4	11	16	7	*Song post.* Bracken, sparse ground vegetation, or even a small bare patch in Phase 4 for nest
Hobby (*Falco s. subbuteo*)	13	.	1	3	9	*Old nest* in almost or completely isolated tree. Phase 1 apparently avoided owing to scarcity of suitable food
Kestrel (*Falco t. tinnunculus*)	5	.	2	.	3	*Old nest or hole* in a tree. Phase 1 apparently avoided owing to scarcity of suitable food
Wild duck (Mallard) (*Anas p. platyrhyncha*)	11	.	.	.	11	*Thick ground vegetation* for nest, within a third of a mile of *water*. A greater distance than this is exceptional
Teal (*Querquedula c. crecca*)	3	.	.	.	3	
Snipe (*Capella g. gallinago*)	7	.	.	.	7	*Thick ground vegetation* for nest. In or near a *marshy area*
Redshank (*Tringa totanus britannica*)	3	.	.	.	3	
Curlew (*Numerius a. arquata*)	14	.	.	5	9	*Thick or moderately thick ground vegetation* for nest. In or near a *marshy area*
Lapwing (*Vanellus vanellus*)	32	19	12	1	.	*Sparse or absent ground vegetation.* Seldom breeding on a heath for more than the first 4 years after a fire. Not far from *marsh or water*
Stock dove (*Columba oenas*)	5	1	.	1	3	*Hole* for nest. In a tree or on the ground
Red-legged partridge (*Alectoris r. rufa*)	3	.	.	.	3	*Thick ground vegetation* for nest
Common partridge (*Perdix p. perdix*)	2	.	.	.	2	
Pheasant (*Phasianus colchicus*)	6	.	.	.	6	*As above*, but always on a heath with *trees* (for roosting)

of the surrounding feeding area. The fired areas are well defined, one from another, with sharp boundaries where the fire was checked, and inside such boundaries the *general* environment is constant, if the whole of the territory is taken, for Phases 1–3. Phase 4, however, is of long duration (if not fired) and parkland and scrubland encroach here and there. This phase becomes rich in species lists and very varied; but for a general survey such as is being attempted in this paper, it is all included under the one heading of Phase 4—maximum *Calluna-Erica* growth (minimum of 8 years after burning), with scattered *Ulex europaeus* bushes and *Betula* and *Pinus* trees. The influence of these last has already been discussed. (As this paper is devoted to heathland birds, Phases 5 and 6 are omitted; a woodland community being found therein.)

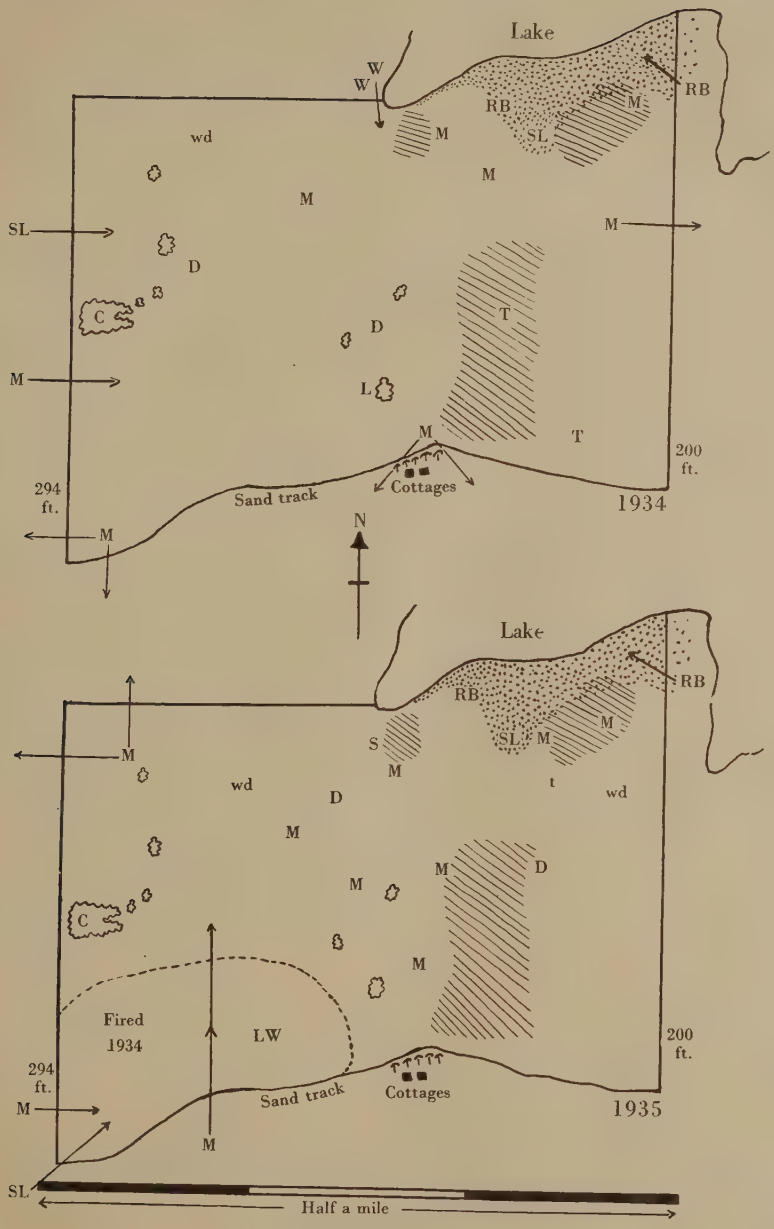
Very occasionally a bird will nest close to a boundary and obtain some of its food across the border (see, for example, the meadow pipit and skylark near the fired area on map 2). In such cases the nest position is taken as the limiting factor.

Secondly, the writer wishes again to stress that he refers only to birds on the Surrey Greensand heath, and not to the general distribution of such birds over the whole of their ranges. He also wishes to point out that he discusses only the distribution in the breeding season. A bird can greatly extend its range when it is not tied down by its inherited behaviour to building a certain type of nest in a certain type of place or to the neighbourhood of a song post. A Dartford warbler, for example, can inhabit the same heath for the whole year; but, unless there is a bush present, a linnet can live on it only for 9 months.

Two maps are reproduced of a 100-acre section of typical Phase 4 Surrey Greensand heath, showing the nest distribution in 1934 and 1935. These give some idea, in miniature, of the distribution as a whole. For example: the reed bunting, wild duck and teal are confined to the proximity of the lake; the former near a marsh. The lapwing comes in as a breeding species so soon as there is a newly fired patch near to marsh or water. Meadow pipits and skylarks, however, even though they show their ability for feeding on the burnt ground, do not nest there. The chaffinch is at the end where the gorse bushes are most numerous, and the tree pipits (absent in 1935) at the end where there are most trees.

Maps 1 and 2. The maps show the nest distribution on a 100-acre section of typical Phase 4 Surrey Greensand heath during early May on two consecutive years.

C = Chaffinch; D = Dartford warbler; L = Linnet; M = Meadow pipit; RB = Reed bunting; S = Stonechat; SL = Skylark; LW = Lapwing; T = Tree pipit; W = Wheatear; t = Teal; wd = Wild duck. The initials mark the approximate positions of the nests. Arrows indicate birds nesting within the section but obtaining part of their food outside its boundaries (or vice versa). Cross-hatch = Codominant trees (*Pinus* and *Betula*). Stipple = Codominant grass; ⌒ = Bushes of *Ulex europaeus*. The remainder is *Calluna-Erica* phase with subdominant *Ulex nanus*.


Lake
W
W
RB
RB
M
M
wd
M
M
SL
M
D
C
D
T
M
L
M
T
200
ft.
294
ft.
Sand track
Cottages
1934
M
N
Lake
RB
RB
M
S
SL
M
M
M
wd
D
t
wd
M
M
D
M
C
M
Fired
1934
LW
200
ft.
294
ft.
M
Sand track
Cottages
1935
M
SL
Half a mile

Maps 1 and 2

The grass straggles back a good distance from the lake half-way along its shore (owing to damper ground), and there the pair of skylarks nested (those outside the area being in sparse, much trampled heather); but it finishes abruptly at the corner, and the stonechats are just back into the dominant heather and breeding in the vicinity of a small group of birches which the male can use as a song post. The wheatears are on a "lawn" of close rabbit cropped turf, too damp in winter for a successful heather invasion.

5. Concluding remarks

In the preceding pages an attempt has been made, as the result of analysing the habitats of many individual pairs of heathland birds, to put down on paper, and to discuss, the common factors in the various species-series of territories; stressing what appear to be the key features. When several such features continually appear, it is difficult to know whether it is one, a combination of several, or the relationship of one to another one or to several. At times it may well be the relation of one to the environment as a whole.

"The exception proves the rule" is, perhaps, classed with the worst of the platitudes; but at least it is true when correctly interpreted. When the birds discussed in this paper are studied in situations remote from heathland, the "exceptional" (for the heathland worker) environment may be found to "prove the rule" by one or several of the old heathland features cropping up again.

Wheatears, for example, are, in the south of England, most numerous on the chalk hills, and there one associates them with the close-cropped turf around rabbit warrens. Naturally, the holes for nesting are of extreme importance; but there are other holes, in walls for example, which are seldom if ever used, and one begins to wonder whether the actual fact of the shortness of the turf round the burrows is of any importance, when it is remembered that, on a Surrey heath, the wheatear is among the first colonizers of a fired area but leaves in a few years when the heather begins to attain a rich growth again—unless it can find a bare patch. Even in Shetland and the Outer Hebrides, where wheatears are perhaps the commonest of the smaller Passerines, many more are to be found on the really bare hillsides than anywhere else, even though the cracks and crannies in which they nest are plentifully distributed.

Can it be that "hole in relation to an environment of bare ground" rather than just plain "hole" presents to the wheatear the picture of the perfect breeding territory?

6. Summary

1. This paper deals with bird distribution on Surrey Greensand heaths, with reference where possible to the botanical succession following a fire. Some of the points raised have been already mentioned or discussed for other types of environment; notably by Lack (1933).

2. The botanical succession on Surrey Greensand heaths is given; roughly divided into six main phases. The last two phases—*Betula* and *Pinus*—seldom obtain, owing to the preceding phase—*Calluna-Erica-Ulex*—being so often subject to fire.

3. A general discussion on the bird distribution follows. Special attention is given to the effect of grass; possible ecoclimatic influence; trees and song posts; bushes; dampness of the heath and proximity to water. Of the birds, most mention is made of the meadow pipit, tree pipit, woodlark, skylark, nightjar and wheatear, all of which are particularly interesting in their choice of habitat.

4. An analysis of breeding territories is then attempted, in which all the usual heathland breeding birds are tabulated and the limiting factors in their distribution are stressed. Maps are given of the bird-distribution on a typical Phase 4 Surrey heath.

5. In the concluding remarks the point is raised of what, to the bird, presents the picture of the suitable breeding territory. Is it the one or few key features, or is it such features in their relation to the environment as a whole?

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APPENDIX

Plant names used in text

Betula sp.	Birch
Calluna sp.	Common ling
Cladonia spp.	Reindeer "moss" (lichen)
Crataegus oxyacantha	Hawthorn
Drosera sp.	Sundew
Erica cinerea	Bell heather
Erica tetralix	Cross-leaved heath
Molinia coerulea	Purple melic-grass, or bent
Pinus spp.	Pines of several species
Pinus sylvestris	Scots pine
Pteridium aquilina	Bracken
Polytrichum juniperinum	Juniper-leaved hair-moss
Rosa sp.	Rose
Rumex acetosella	Sheep's sorrel
Ulex europaeus	Common furze or gorse
Ulex nanus	Dwarf furze or gorse

ON THE HOLOCENE MARINE FAUNA FROM THE IMPLEMENTIFEROUS DEPOSITS OF ISLAND MAGEE, COUNTY ANTRIM

By D. F. W. BADEN-POWELL

CONTENTS

		PAGE
1.	Introduction	86
2.	Report on the Foraminifera, by W. A. Macfadyen	87
3.	Mollusca	91
4.	Conclusions	95
5.	Summary	96

1. Introduction

The north-eastern part of Ireland has long been famous for the sequence of Holocene deposits which is to be found there, and for the relation of that sequence to evidence of occupation by Neolithic man. Our knowledge of this area is mostly due to the well-known work of Lloyd Praeger, supported by studies of the Foraminifera by Joseph Wright, and all subsequent work has been built upon this foundation.

The general sequence of the deposits worked out by Praeger is as follows (1893, p. 212):

Latest. 6. Raised Beach. Early Neolithic.
Upper Estuarine Clay.
5. Lower Estuarine Clay.
4. Submerged peat (with hazel nuts).
3. Sands and gravels.
2. Re-assorted boulder clay.
Oldest. 1. Boulder clay.

The deposits which were especially fossiliferous were the raised beach and the Upper and Lower Estuarine Clays, and the distinction, especially between the two clays, was based by Praeger on the nature of the marine Mollusca (1893, pp. 243–89), of which over 200 species were identified. Praeger also emphasized that the assemblage differed distinctly from that of the earlier Glacial beds, in which *Leda*, *Astarte* and *Trophon* are the commonest genera, whereas *Tapes* and *Venus* were especially typical of the Holocene deposits (1893, p. 220). The warm climate represented by the later Holocene shells was early recognized by Praeger (1893), and was later analysed in greater detail (1898, pp. 45–51). The raised beach at the top of the sequence had been dated as "Early Neolithic" by Coffey & Praeger (1904), the significance of the implements having been pointed out by Du Noyer (1869), but apart from dating

by the archaeological finds, the fossiliferous layers in the Holocene beds can be distinguished from the earlier Pleistocene by the nature of the marine Mollusca, and these fossils can be used further to distinguish between the Upper and Lower Estuarine Clays within the Holocene series.

The true "Neolithic" age of some of the implements was doubted (Smith, 1911; Knowles, 1914), and in more recent years our knowledge of the archaeological dating of the deposits has been enlarged by the discovery by Burchell of pre-Neolithic implements in the Holocene deposits which are earlier than the raised beach. These finds were chiefly described in three papers (Burchell, 1931; Burchell & Reid Moir, 1932, and Burchell, 1934). The last of these describes a sequence on the west side of Island Magee, Co. Antrim, from which the marine fauna discussed in the present paper was extracted. The sequence was as follows:

Raised beach gravels.
Black sand.
"Estuarine Clay" (sample 3).
Black sand.
Subangular black gravel.
Black sand (sample 2).
Subangular black gravel (sample 1).
Land-surface, with tree roots and hazel nuts.
Boulder clay.

The land-surface is situated at a depth of 1 ft. 6 in. below Low Water Mark of ordinary tides, and the thickness of the overlying deposits is 10 ft. (MS. letter from Burchell.) The implements found in the clay and gravel below the raised beach horizon were originally considered by Burchell to belong to some late phase of the Magdalenian (1931, 1932), but later he ascribed them to the Mesolithic Forest Cultures, for more direct comparison with the cultural stages of Northern Europe (1934, p. 366).

The samples sent were rich, especially in the remains of Foraminifera and Mollusca, a comparison can therefore be made between the fauna in these samples and that studied by Praeger and Wright. We wish to thank Mr Burchell for putting this material at our disposal, and we also thank Mr C. C. A. Monro, Mr D. J. Scourfield and Mr T. H. Withers for kindly giving their opinion on Serpulids and other forms which were washed out of the samples.

2. Report on the Foraminifera

By W. A. Macfadyen

The following species have been identified, and the numbers at the head of each column refer to the layers indicated in the sequence studied by Burchell. There are two columns for sample 2, because there was originally some doubt in our minds about the distinction between samples 1 and 2, but Burchell

kindly put further material from sample 2 at our disposal, and the fauna of the material queried as sample 2 was then seen to be unlike that of sample 1. For instance, there is an absence of all species of *Lagena* in sample 1. It resembles that of sample 2, but is appreciably richer, approaching that of sample 3. Significant common species suggesting that it is actually sample 2 are *Triloculina oblonga*, *Massilina secans* and *Cibicides pseudoungerianus*.

The abbreviations used in this list, corresponding to the Roman numeral symbols for frequency used by Foraminifera experts are: v.r. = very rare; r. = rare; f. = frequent; c. = common; a. = abundant.

Samples...	1	2	? 2	3
Spiroloculina excavata d'Orbigny	—	v.r.	v.r.	—
S. planulata (Lamarck)	—	r.	v.r.	—
Quinqueloculina angulata (Williamson)	—	v.r.	r.	—
Q. bicornis (Walker & Jacob)	v.r.	v.r.	r.	v.r.
Q. cliarensis (Heron-Allen & Earland)	—	v.r.	v.r.	—
Q. fusca Brady	v.r.	v.r.	v.r.	—
Q. laevigata d'Orbigny	r.	f.	r.	—
Q. lamarckiana d'Orbigny	f.	f.	f.	f.
Q. schlumbergeri (Heron-Allen & Earland)	—	—	v.r.	v.r.
Q. sclerotica Karrer	c.	c.	c.	r.
Q. seminulum (Linné)	—	—	—	f.
Q. subrotunda (Montagu)	f.	c.	c.	r.
Triloculina circularis Bornemann	—	r.	r.	—
T. oblonga (Montagu)	—	f.	f.	—
T. rotunda (d'Orbigny)	v.r.	—	—	—
T. tricarinata (d'Orbigny)	v.r.	v.r.	r.	v.r.
T. trigonula (Lamarck)	—	v.r.	f.	r.
Massilina secans (d'Orbigny)	—	r.	f.	—
,, var. *tenuistriata* Earland	—	—	—	v.r.
Cornuspira involvens (Reuss)	v.r.	f.	f.	r.
Trochammina inflata (Montagu)	—	v.r.	r.	v.r.
T. ochracea (Williamson)	—	—	—	v.r.
T. plicata (Terquem)	—	—	—	v.r.
T. squamata Jones & Parker	—	—	—	f.
Textularia gramen d'Orbigny	—	r.	v.r.	r.
T. sagittula Defrance	—	v.r.	—	—
Bulimina marginata d'Orbigny	v.r.	v.r.	r.	r.
B. pupoides d'Orbigny	—	v.r.	r.	r.
Buliminella elegantissima (d'Orbigny)	—	—	—	r.
Virgulina fusiformis (Williamson)	—	—	—	f.
Bolivina difformis (Williamson)	—	—	v.r.	r.
B. pseudoplicata Heron-Allen & Earland	—	r.	f.	f.
B. variabilis (Williamson)	v.r.	f.	f.	f.
Cassidulina crassa d'Orbigny	—	—	v.r.	r.
C. laevigata d'Orbigny	—	—	—	v.r.
Lagena bicarinata (Terquem)	—	—	—	v.r.
L. catenulata (Jeffreys, M. S. Williamson)	—	f.	f.	r.
L. clavata d'Orbigny	—	v.r.	r.	r.
L. costata Williamson	—	—	v.r.	v.r.
L. filicosta Reuss	—	v.r.	v.r.	v.r.
L. globosa (Montagu)	—	v.r.	—	v.r.
L. gracilis Williamson	—	—	—	v.r.
L. gracillima (Seguenza)	—	—	—	v.r.
L. hexagona Williamson	—	—	v.r.	v.r.
L. laevis (Montagu)	—	—	v.r.	f.
L. lineata (Williamson)	—	v.r.	v.r.	v.r.
L. lucida (Williamson)	—	r.	f.	f.
L. lyellii (Seguenza)	—	—	v.r.	—
L. marginata (Walker & Boys)	—	v.r.	v.r.	r.
L. marginato-perforata Seguenza	—	—	—	v.r.
L. orbignyana (Seguenza)	—	v.r.	—	v.r.
L. perlucida (Montagu)	—	—	v.r.	v.r.

Samples...	1	2	? 2	3
Lagena pulchella Brady	—	—	v.r.	—
L. scalariformis (Williamson)	—	v.r.	f.	—
L. semistriata Williamson	—	—	v.r.	r.
L. substriata (Williamson)	—	—	—	r.
L. sulcata (Walker & Jacob)	—	v.r.	r.	—
L. williamsoni (Alcock)	—	f.	f.	f.
Nodosaria pyrula d'Orbigny	—	—	—	v.r.
N. scalaris (Batsch)	—	—	v.r.	v.r.
Dentalina communis d'Orbigny	—	—	—	v.r.
Vaginulina legumen (Linné)	v.r.	—	—	v.r.
Cristellaria crepidula (Fichtel & Moll)	—	—	—	v.r.
C. gibba d'Orbigny	—	—	—	v.r.
C. rotulata d'Orbigny	—	—	v.r.	—
Guttulina lactea (Walker & Jacob)	v.r.	v.r.	v.r.	—
G. problema d'Orbigny	—	—	v.r.	—
Uvigerina angulosa Williamson	—	—	v.r.	v.r.
Globigerina bulloides d'Orbigny	v.r.	v.r.	r.	r.
Patellina corrugata Williamson	—	v.r.	v.r.	r.
Discorbis globularis (d'Orbigny)	v.r.	f.	f.	f.
D. mediterranensis (d'Orbigny)	—	v.r.	f.	—
D. millettii (Wright)	—	v.r.	r.	v.r.
D. nitidus (Williamson)	—	—	—	r.
D. obtusus (d'Orbigny)	—	v.r.	r.	f.
D. orbicularis (Terquem)	v.r.	v.r.	v.r.	—
D. parisiensis (d'Orbigny), Brady	—	v.r.	r.	v.r.
D. peruvianus (d'Orbigny), Heron-Allen & Earland	—	r.	f.	f.
D. praegeri (Heron-Allen & Earland)	v.r.	r.	f.	f.
D. tuberculatus (Balkwill & Wright)	—	—	—	v.r.
D. turbo (d'Orbigny), Brady	—	—	v.r.	—
Lamarckina haliotidea (Heron-Allen & Earland)	—	—	—	r.
Cibicides lobatulus (Walker & Jacob)	f.	f.	f.	f.
C. pseudoungerianus (Cushman)	—	f.	r.	—
C. refulgens (Montfort)	—	—	v.r.	—
Planorbulina mediterranensis d'Orbigny	—	r.	f.	r.
Acervulina inhaerens Schultze	v.r.	v.r.	f.	—
Rotalia beccarii (Linné)	f.	r.	f.	a.
R. perlucida Heron-Allen & Earland	—	—	—	v.r.
Nonion depressulus (Walker & Jacob)	v.r.	r.	f.	f.
N. pauperatus (Balkwill & Wright)	—	—	v.r.	v.r.
N. pompilioides (Fichtel & Moll)	—	v.r.	—	v.r.
Elphidium advenum (Cushman)	v.r.	v.r.	—	—
E. crispum (Linné)	a.	a.	a.	c.
E. excavatum (Terquem)	f.	f.	f.	v.r.
E. incertum (Williamson)	v.r.	—	—	—
„ var. *clavata* (Cushman)	v.r.	—	—	r.
E. macellum (Fichtel & Moll)	r.	r.	r.	f.
E. oceanense (d'Orbigny)	—	—	—	f.
Total species 99	27	56	68	73

The increasing variety of Foraminifera from sample 1 with 27 species, through sample 2 with 56 species, to sample 3 with 73 species is largely due to the type of the deposits. Sample 1 is a gravel with sand, in which the smaller species are not found; the finer sand of sample 2 yields a better selection, while the marl of sample 3 is a highly Foraminiferal deposit well calculated to preserve the smallest species.

The fauna shows a shallow water assemblage of recent forms, most of which have been recorded as living off this coast at the present day, mainly by Wright. Of apparent differences a part is certainly due to divergences in nomenclature. Compared with various Quaternary and Holocene faunas from Northern Ireland recorded by Wright in his many papers, the present fauna

resembles most nearly those from Holocene clays of Magheramorne and Limavady, Co. Derry (J. Wright, 1911 *b*).

The faunal lists in the following papers by Wright have been compared with the Magee Foraminifera: 1877, 1880, 1886, 1909, 1911 *a*, *b*.

As regards climatic indication, the Magee Foraminifera do not appear to show any difference from present day conditions. The boreal species *Elphidium arcticum* was not recorded; it might have been expected, had the climate been appreciably colder, since it is recorded by Wright and by Gough in various Glacial deposits of Northern Ireland.

With regard to salinity indication, there is nothing to suggest other than purely marine conditions of deposition. *Elphidium crispum* is abundant, and this is a species intolerant of brackish water. Compared with the deposits in the Cambridgeshire Fenlands which were laid down in brackish water, the number and variety of Miliolidae are most marked, while the typical brackish-water indicators, such as *Quinqueloculina fusca*, *Trochammina inflata* and *Trochammina macrescens*, are either wanting, or very rare. No specimens derived from older rocks were recognized in any of the Magee samples.

Numbers of Ostracoda and Polyzoa were found in most of the samples. In the Fenlands, unidentified Ostracoda were found to have no significance as salinity indicators; but Polyzoa were restricted to the most nearly marine deposits. On the question of the tolerance of Foraminifera to brackish water, Brady's pioneer paper may be consulted (1870), but the writer has been guided largely by his own work on the subrecent foraminiferal faunas from the brackish-water deposits of the Cambridgeshire Fenlands (e.g. Macfadyen, 1933).

Notes on the Foraminifera

The nomenclature of various species assigned here to the genus *Discorbis* is difficult and involved. Since no attempt at rectification can be attempted here, Heron-Allen & Earland's usage in their Clare Island memoir is adopted (1913, pp. 110 *et seq.*). With this interpretation, the following of Brady's figures in his Challenger Report are considered illustrative:

D. peruvianus (d'Orbigny), Brady's *D. vilardeboana* (d'Orbigny), Pl. LXXXVIII, Fig. 2.
D. mediterranensis (d'Orbigny), Brady's *D. vilardeboana* (d'Orbigny), Pl. LXXXVI, Fig. 9.
D. parisiensis (d'Orbigny), Brady's *D. parisiensis* (d'Orbigny), Pl. XC, Figs. 9–12.

From sample 3 came three normal and two plastogamic specimens of *Discorbis millettii*. One of the latter came apart, showing a brood of young inside the tests, the internal structure of which had been resorbed. The young specimen which was extracted possessed three complete chambers and traces of a fourth.

The nomenclature of the striate species of *Lagena* is somewhat involved. To define the identifications, the following figures may be referred to in Williamson's *Recent Foraminifera of Great Britain* (Ray Society, 1858).

Lagena filicosta Reuss, Williamson's Fig. 10, *L. vulgaris* var. *striata*.
L. perlucida (Montagu), Williamson's Fig. 7, *L. vulgaris* var. *perlucida*.

Quinqueloculina sclerotica Karrer.

The record of this species here includes both the angular- and the round-edged forms, which grade one into the other imperceptibly. The round-edged forms are recorded separately under the name *Q. contorta* d'Orbigny. I am much indebted to Mr Arthur Earland for assistance in the identification of several of the Miliolidae recorded, and for his kindness in reading the manuscript of these notes.

The Foraminifera recorded above are preserved on nine slides, numbered 184, 185, 185 *a*, 186, 186 *a*, 186 *b*, 188, 188 *a*, and 188 *b*, at present in the author's own collection. They will eventually be deposited in the Sedgwick Museum, Cambridge.

3. Mollusca

The samples from the section on Island Magee were treated in the following way. The sands and gravels (samples 1 and 2) were sieved gently, the larger stones and shells having been picked out. It was found that gentle sieving did not damage the shells, even such delicate forms as *Turtonia* coming through unscathed. The clay (sample 3) was washed, and both the floating forms (mostly *Rissoa*, *Lacuna* and *Skeneopsis*), and the shells left behind after the silt grade had been washed off, were collected. The gravel (sample 1) was also washed before sieving, so as to remove pellets of clay which contained small shells, and which were too large to go through the sieve (approximately 1 mm. mesh). A fine camel-hair brush was used for picking out the small shells, both those which floated and those which remained on the bottom of the dish, and glass microscope slides were found convenient objects on which to dry them.

The question of nomenclature is one of the most difficult and annoying problems which confronts one in work of this kind, but the course adopted in the present instance has been to use the specific names of R. Winckworth's *British Marine Mollusca* (1932); but certain divergences are made from this list in the matter of generic names. This has been done, because it is felt that well-known names such as *Lucina* and *Tapes* are more valuable in such a discussion as this than their new-found substitutes, *Phacoides* and *Paphia*.

For the purpose of the list which follows, the shells from the two samples labelled "sample 2" are put together in one column, as their faunas are nearly enough the same. The numbers 1–3 refer to the samples so marked in the sequence studied by Burchell (p. 87). The abbreviations used are: a. = abundant, c. = common, r. = rare.

The identification of some of these species was uncertain, as they were represented by young shells only, as will be seen from the list. It is suggested that only those species which are common, or of which the identification is sure, can be used as climatic or ecological indicators.

Samples...	1	2	3
Anomia sp., young	r.	r.	r.
Pecten maximus (Linné)	—	—	r.
Chlamys opercularis (Linné)	—	r.	r.
Mytilus edulis Linné	r.	—	—
Modiolaria, cf. *costulata* (Risso)	—	r.	r.
M. discors (Linné)	—	r.	r.
Nucula nucleus (Linné)	—	—	r.
Leda minuta (Müller), ? var. *brevirostris* Jeffreys	—	—	r.
Axinus, cf. *ferruginea* Winckworth	r.	r.	r.
A. flexuosus (Montagu)	—	—	c.
Lucina borealis (Linné)	r.	r.	r.
Lasaea rubra (Montagu)	c.	c.	r.
Turtonia minuta (Fabricius)	a.	a.	r.
Montacuta ferruginosa (Montagu)	—	—	r.
M. bidentata (Montagu)	r.	—	r.
Cardium edule Linné	—	—	r.
C. exiguum Gmelin	—	—	r.
Tapes pullastra (Montagu), young	r.	—	—
Tapes, cf. *decussatus* (Linné) var. *fusca* (Gmelin), fragment	—	r.	—
Circe minima (Montagu)	—	—	r.
Tellina ? *tenuis* da Costa, fry	—	r.	—
Tellina ? *donacina* Linné, fry	—	r.	—
Tellina sp. ?	—	—	r.
Abra alba (S. Wood)	r.	r.	c.
Ensis siliqua (Linné)	r.	—	—
Mya truncata Linné ?	—	—	r.
Corbula gibba (Olivi)	—	r.	r.
Saxicavella jeffreysi Winckworth	—	—	c.
Patella vulgata Linné	—	r.	—
Helcion pellucidum (Linné), young	—	c.	—
H. laevis (Pennant)	—	r.	—
Tectura sp., young	r.	—	—
Gibbula cineraria (Linné)	c.	a.	c.
Lacuna pallidula (da Costa)	c.	c.	r.
L. vincta (Montagu)	r.	—	a.
Littorina littorea (Linné)	—	r.	—
L. saxatilis (Olivi) (=*rudis*)	a.	a.	r.
L. littoralis (Linné) (=*obtusata*)	a.	a.	r.
? *Hydrobia ulvae* (Pennant), young	r.	r.	r.
Rissoa parva (da Costa)	r.	r.	—
,, var. *interrupta* Adams	c.	c.	r.
R. lilacina Récluz	r.	—	—
R. membranacea Adams	r.	—	r.
Onoba striata (Adams)	a.	a.	a.
Skeneopsis planorbis (Fabricius)	a.	a.	r.
Omalogyra atomus (Philippi)	—	r.	r.
? *Eulimella* sp., reversed	r.	—	—
? *Cerithiopsis metaxae* (Chiaje)	—	—	r.
? *Purpura lapillus* (Linné), fry	—	r.	—
? *Buccinum undatum* Linné, fragment	r.	—	—
Retusa alba (Kanmacher)	—	r.	r.
Leucopepla (*Melampus*) *bidentata* (Mont.)	—	r.	—

Climatic equivalent. We can say of this assemblage as a whole, that there is no sure indication that either samples 1, 2 or 3 were laid down under climatic conditions differing from those of to-day. One indicator which suggests a possibly warmer climate is *Modiolaria costulata*, but the identification of this species is only provisional, as it is based on young shells. These measured only up to 3 mm. broad, whereas the adult of this species should measure 10 mm. By comparison with the Barlee Collection at Oxford, however, the Magee shells

agree both in colour and in the position of the beak. The only species found in the Magee material which agrees with the typically warm shells cited by Praeger (1898, pp. 49, 50) is "*Tapes decussatus*", but it is unfortunate that again the identification of this species is uncertain, as only one small fragment was found. It is only possible to say then, that this collection from Magee shows no indication of cold conditions, but doubtfully shows slight indications of a warmer climate. Taking a broad view, the general association is that found on this coast at the present day.

Ecology. When we come to consider the conditions under which the deposits were laid down, we are on safer ground, but even here the evidence is to some extent contradictory. On the whole, however, the abundance of *Littorina* in samples 1 and 2, and the comparative frequency of *Abra alba* in sample 3, suggests strongly that sample 3 was laid down in deeper water than the lowest deposits in the section. It is impossible to make anything like an accurate estimate of the depth, but samples 1 and 2 might have been deposited between tide-marks, and sample 3 was probably deposited in not more than 2 or 3 fathoms; but the frequency of *Axinus flexuosus* in the clay (sample 3), sometimes with the two valves joined, suggests a depth of at least 3 fathoms. These figures must however be taken as an indication of the depths rather than as an accurate estimate.

By far the most abundant species among the small Mollusca from samples 1 and 2 are *Lasaea rubra*, *Turtonia minuta* and *Onoba striata*. All three of these species suggest luxuriant growth of seaweed in the neighbourhood when they were living, and it is interesting in this connexion that Praeger mentions that luxuriant growth of sea-weed has been suggested as contributing to the formation of the Estuarine clay (1893, p. 216), thus explaining its occurrence on exposed parts of the coast, where one would expect the clay-grade to be removed by wave-action. *Turtonia* was, however, much rarer in sample 3, but as this shell may only happen to be scarce in the particular sample taken, it is not easy to say how far the presence of these species in abundance supports this theory of the formation of the clay.

It is certainly not possible for clay to form on an open coast without some protection against wave-action. Praeger has suggested (Coffey and Praeger, 1904) that some of the Holocene clay at the Curran at Larne, which is just across the bay from the Magee site, was laid down behind a protecting underwater sandbank, and it is possible that this sandbank also damped the wave action which would have removed the clay from the site on Island Magee, thus allowing the clay to be deposited.

Counts were made of the adult shells in the samples; but it must be remembered that these figures only refer to the particular samples, and it is not known how typical they may be of the deposits as a whole. For various reasons, the large and small shells are listed separately. The absolute frequency of the shells can be judged from the size of the samples.

Samples 1 and 2 were not weighed, but the volumes were approximately: sample 1, 1290 c.c.; sample 2, 1440 c.c. The weight of clay used from sample 3 was about 14 lb. for the small shells, and 30 lb. for the large.

Counts of larger shells

		Actual numbers counted		
Species	Samples...	1	2	3
Littorina saxatilis		40	8	6
L. littoralis		26	15	3
Gibbula cineraria		4	12	8
Lacuna pallidula		6	17	5
L. vincta		1	—	20

The main significance of this count is that *Littorina* is most common in the gravel (sample 1), whereas *Lacuna vincta*, which inhabits slightly deeper water than *Littorina* in the living state, is more common in the clay (sample 3).

Counts of smaller Lamellibranchs

		Actual number of valves		
Species	Samples...	1	2	3
Turtonia minuta		130	280	4
Lasaea rubra		12	50	3
Axinus, cf. *ferruginea*		1	10	2

Counts of smaller Gasteropods

		Actual number counted		
Species	Samples...	1	2	3
Onoba striata		107	176	80
Skeneopsis planorbis		71	138	11
Rissoa interrupta		53	30	5
R. membranacea		14	—	12
R. parva		2	15	—

These figures show that *Turtonia minuta* is very much more common in samples 1 and 2 than in sample 3, and that *Onoba striata* is consistently the most common of the smaller Gasteropods in all the samples.

All the marine Mollusca from these Island Magee samples have been deposited in the Oxford University Museum.

During the process of washing for Foraminifera and small Mollusca, Serpulid worms and Ostracoda were also found. Mr C. C. A. Monro reports that the Serpulid tubes are not easy to identify, beyond the fact that they are Spirorbids. Among the Ostracoda, Mr D. J. Scourfield has identified *Cythere albomaculata*, by comparison with Brady's Monograph, and he quotes Brady as saying that this form is found "in the littoral and Laminarian zones, and running to a considerable distance up the tidal rivers". Mr Scourfield also observes that all the Ostracoda from the Magee samples are marine forms, and

most of them are species of *Cythere*, or closely allied genera. Fragments of Decapod Crustacea submitted to Mr T. H. Withers were too incomplete for any definite determination.

4. Conclusions

The main task here is to decide as far as possible where the deposits, from which Burchell obtained the implements, come in Praeger's type sequence, and the evidence both of the Foraminifera and the Mollusca in the present collections is in close agreement as far as it goes.

The first point made by Praeger (1893, p. 220) is that in Northern Ireland shells typical of a cold climate, such as *Leda pernula*, *Astarte borealis*, *Tellina calcarea* and *Trophon clathratus*, are never found in the series of clays and gravels which overlie the peat (with hazel). These shells are also absent in all the samples sent by Burchell, and the cold indicator *Elphidium arcticum* was also absent from the Foraminifera, even from the lowest part of the sequence. Therefore from the palaeontological point of view, *the whole of Burchell's sequence above the boulder clay belongs to the Holocene.* This point is emphasized here so as to make it quite clear that Burchell's implements showing an Upper Palaeolithic tradition are not associated with a colder climate than that of the present day, as far as the marine deposits are concerned.

It is most unfortunate that the term "Estuarine Clay" was originally chosen for the Holocene clays of Northern Ireland, because the fauna is certainly not estuarine, in the sense of having lived in brackish water, and the Foraminifera and the Mollusca in the present collection testify to the truly marine conditions under which the deposits containing this fauna were laid down. But the term "Estuarine Clay" has been so long in use that we will not alter it here. Praeger's distinction between the Upper Estuarine and the Lower Estuarine Clays was based on the depth represented by the molluscan assemblage. He considered (1893, p. 214) that the Lower Clay was originally deposited in the tidal zone, perhaps towards low-water mark, typical shells being *Tapes decussatus*, *Cardium edule*, *Scrobicularia piperata*, and a few others. The Upper Clay, with *Abra* (*Scrobicularia*) *alba*, *Thracia convexa*, and other species which now live below low-water mark, he considered to represent a depth of water of from 1–5 fathoms, but there was often a gradual passage from the tidal to the deeper deposit.

The Foraminifera in the present collection resemble most nearly Wright's lists from Magheramorne and Limavady. From the Mollusca, the Limavady clay is classified as intermediate in type between the Upper and Lower Estuarine Clays. Both these clays are found at Magheramorne (Praeger, 1893, p. 226). As far as the Mollusca from Island Magee are concerned, the assemblage in samples 1 and 2 suggest intertidal conditions, with a tendency towards Low Water Mark, and the assemblage in sample 3 slightly deeper water (? about 3 fathoms), containing a mixture of intertidal forms (*Littorina*) with *Abra alba*

and *Lacuna vincta*. It is not possible to make a more accurate estimate of depth of deposition, either from the Foraminifera or from the Mollusca; but it is probable from the nature of the shells in the samples from Magee that *the lowest sand and gravel in Burchell's sequence (samples 1 and 2) are of the same age as Praeger's Lower Estuarine Clay, and Burchell's Estuarine Clay is intermediate in age between Praeger's Lower and Upper Clays.*

5. Summary

An examination of the Foraminifera and Mollusca from a sequence of implementiferous deposits on the west side of Island Magee, Co. Antrim, shows an increasing depth of deposition from the base towards the upper part of the section. This result makes direct comparison possible with the classical sequence worked out by Praeger for the Holocene of Northern Ireland. The suggested correlation is as follows:

Praeger	Burchell
Raised beach and Upper Estuarine Clay	Raised beach
Intermediate Estuarine Clay	Lower Estuarine Clay
Lower Estuarine Clay	Sand and Gravel
Submerged peat	Submerged peat

If this correlation is correct, the flint industry which Burchell found in the sand and gravel is the equivalent in age of Praeger's Lower Estuarine Clay.

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FLUCTUATIONS IN NATURAL POPULATIONS OF COLLEMBOLA AND ACARINA

By JOHN FORD

(*Hope Department, University Museum, Oxford*)

(*With Plates 4 and 5 and 3 Figures in the Text*)

1. Introduction

A considerable amount of attention has been paid to populations of Collembola (springtails) and Acarina (mites) which inhabit soil and vegetation in which decay processes are taking place. These populations increase during the winter months when the high moisture content of the environment favours their development. They are especially interesting for ecological investigation in that the curves obtained by sampling them are true population growth curves reaching their maxima by the reproductive efforts of many rapidly breeding generations. Such curves differ from those obtained by sampling insect communities active in summer which represent emergence phenomena and reach their maxima, in most cases, by successive appearances of adults of a single generation from hibernation. Thus with the Collembola and Acarina populations it is possible to investigate population behaviour resulting from the cumulative effect of many generations within a period of a few months. To obtain analogous results with most other groups of terrestrial Metazoa it would be necessary to continue observations over periods of many years.

The most complete study yet available of the fluctuations of populations of Collembola and Acarina is that of Thompson (1924) who took samples of the soil population of pastureland at intervals of 14 days for a period of 2 years. In a curve (p. 367) for the combined population of Collembola and Acarina, Thompson shows that the major trends were as follows: the population commenced to increase in October, 1920; thereafter came peaks in November and January, with alternating minima in December and February: in 1921 the increase began in August, reaching a peak again in November, with subsequent peaks in January and March and with alternating minima in December, February and April.

The population of the winter of 1921–2 was much larger than in the previous year owing, presumably, to an abnormally great amount of precipitation. There appear also to have been minor fluctuations of the Collembola-Acarina population during the summer months. Edwards (1929) demonstrated an increase in the soil population in winter but only took samples at intervals of 3 months, so that lesser fluctuations are not recorded. Both the above surveys were made at Aberystwyth.

Working on soil populations at Oxford (1935) I found a peak occurred in December, followed by a low January population, after which there was some evidence that another increase took place in February. In these surveys it appeared that the fluctuations were confined mainly to the Collembola, the Acarina having but little, if any, share in them. However, Ionescu (1932), working on the fauna of woodland floor litter in Roumania, showed that a double fluctuation, with very marked peaks in October and January, occurred in populations of both Collembola and Acarina. Finally, Frenzel (1936) studied the seasonal fluctuations of similar populations in soil of various meadows in Silesia. (This paper is reviewed by the writer in the *Journal of Animal Ecology*, 1937, 6: 197.) Except in one instance Frenzel's samples were not taken with sufficient frequency to indicate more than the general winter increase in Collembola and Acarina populations. In one curve, however (p. 102), there is an indication that between the maximum of the Collembola population in late October and the minimum in March, there was another lesser peak in January.

There is thus some evidence that during the period of abundance of Collembola and Acarina, which occurs between late autumn and early spring, these populations, in widely separated districts and in different years, undergo certain fluctuations which are a common feature of them all. Hitherto these fluctuations have been attributed, if they have been discussed at all, to environmental changes. If, however, the bimodal form taken by the curves for Collembola and Acarina populations between October and March, which is so marked in Ionescu's data, is characteristic of these populations in general, as it would seem to be, then it is extremely doubtful if environmental change can be responsible. If it were we should have to suppose that in all these cases some violent change in the physical conditions occurred in December or January to cause declines in populations which had been increasing since October, and that in January or February another change took place allowing the population to multiply once more. While it is impossible to assert dogmatically that such changes do not occur, for our knowledge of the physical requirements of these species is not very wide, yet the chances appear to be against it and it would seem advisable to seek another explanation.

The work to which this paper is an introduction was commenced in October 1935 and is concerned with the fauna inhabiting the above-ground vegetation in a community of the grass *Bromus erectus*. This fauna is composed almost entirely of Collembola and Acarina. It was first necessary to confirm that the fluctuations shown in the data of other workers do actually occur and to devise a technique for observing them.

2. HABITAT AND PHYSICAL ENVIRONMENT

The sampling area is about $\frac{1}{2}$ acre in extent and in it the grass *Bromus erectus* is dominant. The only other plant contributing at all markedly to the flora is the moss *Brachythecium purum*. This plant community, which will be

referred to henceforth as the Brometum (Pl. 4, phot. 1) is developed on Coral Rag soil (*p*H 7·4–7·5) lying about 40 cm. deep over the parent rock. The Brometum is situated in an ungrazed field at Headington, about 3 miles north-east of Oxford, lying approximately 1° 11′ 30″ W. by 51° 47′ N. on the Ordnance Survey. Most of this field, which lies at a height of 350 ft., is rather sparsely covered with vegetation in which a species of *Holcus* is dominant. The Brometum occurs as an isolated patch between the *Holcus* area and a third which consists of more or less exposed ground on which occur the moss *Barbula fallax*, rosette plants (mainly *Hieracium pilosella*) and, in winter, the dead stalks of *Poterium sanguisorba*. This latter area separates the Brometum from a wooded valley and copse which have the effect of sheltering it from northerly and westerly winds.

The grass *Bromus erectus* forms tussocks and the population with which we are concerned tends to be concentrated in them. It is therefore necessary to describe the structure of a *Bromus* tussock in its winter aspect, in some detail. These tussocks are separated from one another by from 9 to 12 in. Pl. 4, phot. 2, shows a single tussock in longitudinal section. The dead leaves of the previous summer's growth are blown over in the direction of the prevailing south-west wind, and where they touch the ground form a layer of damp decaying hay (C).

A second region in the tussock is formed partly of dead and partly of living leaves and lies immediately over the stock (B). This region is the most exposed and it offers a shelter to the other regions from evaporation. The third region is composed of the stock (A) made up of living shoots, each of which is surrounded by one or more layers of dead tissue derived from leaves of previous years. This typical tussock structure is permanent except in the face of strong contrary winds, when it breaks down, with disastrous effect on the fauna.

By use of Buxton's dew-point hygrometer (by which relative humidity of air in confined spaces may be measured) and by exposure of wet- and dry-bulb thermometers above and beneath the protecting layer B it is possible to show that in the regions A and C the air has a high moisture content as compared with the external air and that fluctuations in temperature outside the tussocks are only reflected to a slight degree within. Table 1 records the variations between 11.0 a.m. and 3.30 p.m. of wet- and dry-bulb temperatures and saturation deficit inside and outside tussocks (22. x. 36). The difference between the average moisture content inside and outside the tussock is well outside the limits of error. These observations were taken on a uniformly cloudy day. Another set taken when the sun was alternately covered and exposed by moving cloud illustrates even more markedly the shading effects of the outer regions of the tussock. During a period of 1 hour in the afternoon air temperature varied from 6·4 9·6° C. outside the tussock. Inside the variation in temperature was 6·3 7·2° C. The mean saturation deficit outside the tussock was 2·3 g. per cu. m. and within 1·1 g.

Phot. 1. The Brometum.

Phot. 2. Longitudinal section of *Bromus* tussock (for explanation see text).

Table 1. *Half-hourly microclimatic changes inside and outside* Bromus *tussock obtained by exposure of wet- and dry-bulb thermometers. (Saturation deficit obtained by use of Baker's nomogram)*

	Above tussock			Inside tussock. Region A		
Time	Wet bulb ° C.	Dry bulb ° C.	Saturation deficit g. per cu. m.	Wet bulb ° C.	Dry bulb ° C.	Saturation deficit g. per cu. m.
11·0	12·7	15·0	3·1	14·2	15·2	1·5
11·30	12·8	15·0	3·0	13·6	14·6	1·5
12·0	13·0	15·4	3·3	13·8	15·0	1·8
12·30	13·0	15·6	3·6	13·9	15·5	2·3
1·0	13·8	16·3	3·6	14·5	16·0	2·2
1·30	13·0	15·5	3·5	13·9	15·5	2·3
2·0	12·7	14·9	3·0	13·1	14·4	1·8
2·30	12·3	14·4	2·9	12·7	13·9	1·7
3·0	11·7	13·5	2·4	12·3	13·3	1·4
3·30	11·5	12·8	1·7	11·9	12·7	1·1

In as much as Maldwyn Davies (1928) has demonstrated that Collembola succumb very rapidly when the evaporation rate is high and that, moreover, they need for their continued existence to live in contact with moist surfaces, the property of the *Bromus* tussocks of maintaining an environment of high moisture content is of vital importance in the lives of their fauna.

3. Sampling methods

At the outset of this survey it was necessary to devise a technique for the estimation of the density of the fauna. Such a density can be expressed either as "number of organisms per unit area" or as "number of organisms per unit weight of inhabited plant matter". In this work both measures are used.

(1) The average tussock of *Bromus* could be surrounded in an area contained by four stakes, joined by stout wires, forming a rectangle of 20×10 cm. Within this area all vegetation and loose debris was removed from the soil surface with scissors and placed in a linen bag. Four such samples were combined to give the population figure for each date. The fauna was extracted by means of a Berlese funnel, working at a temperature of about 50° C. for 24 hours. The organisms were collected in a beaker of water, on which all species, save a few larvae, float. The method used in counting the samples has already been described (Ford, 1936). The results obtained by this method are expressed as numbers of organisms per sq. m. They do not express, however, the true density of animals in the Brometum, but only in the tussocks: samples were not taken in the spaces between tussocks.

(2) After a few weeks' work with the above method it became evident that many advantages would be gained by using, instead of one large composite sample, a number of small samples which could be extracted and counted separately. The apparatus finally devised is shown on Pl. 5, photos. 3 and 4. It consists essentially of a battery of 12 Tullgren funnels in which the heat is

supplied from above by electrically heated wire coils. The samples are placed in the funnels on the lower tray. The upper component containing 12 metal chimneys, each with its heater, is then fitted above as shown in the photograph. The heaters are made of 1 in. lengths of domestic electric heater radiant wire designed to give a red heat with a current of 200 volts. They are used, however, in this case, with a current of 100 volts. This does not produce a red heat, but yields a temperature of about 50° C. at the level of the funnels.

This apparatus, which is now being used successfully, was not completed in its present form at the time when the data dealt with in this paper were obtained. Instead, a modification of it, in which electric lamps were substituted for the electric coils, was used.

Either 5 or 10 samples were taken for use with these Tullgren funnels and were collected as follows. Only the vegetation in the stock region (A) of the tussocks was used, the remainder being cut away. The samples were collected in corked glass tubes, the whole being weighed before extraction. After extraction the sample was again weighed. This weight of dried grass was used as the unit of reference for density, the results given for these samples being the mean number of organisms per g. of dried grass. It was found useful to obtain an estimate of the loss of water by evaporation from the sample, which was easily done by subtracting the weight of the dried sample plus that of the tube from the original weight of tube and undried sample obtained at the first weighing.

By sampling from various parts of tussocks with the above methods it was possible to analyse the distribution of organisms within individual tussocks. Samples were taken always during the afternoon, between 2 and 4 p.m.; the extraction processes were commenced the same evening and continued till the morning of the next day but one, when the counts were made.

4. Composition of the fauna

Associated with the Collembola and Acarina in the tussocks are other animals which occur less abundantly in the samples. Some of these, i.e. some spiders and the smaller Staphylinidae (Coleoptera), are predators on the fauna with which this paper is concerned. Others, including various Mollusca, two species of Isopoda and a number of Diptera may perhaps be regarded as scavengers, while larvae and adults of other groups are present in the Brometum as hibernators. These are not confined to the tussocks and the Diptera (mainly Borboridae) appear to be associated with vole runs. Collections of these species have been made but consideration of them is reserved for a later publication. There is also an active soil fauna which forms a community separate from that inhabiting the tussocks. The predominating soil species is *Tullbergia* (*Mesaphorura*) *krausbaueri* Born. which does not occur in the tussocks.

Table 2 expresses the relative proportions, during the whole sampling season, of the various components of the tussock fauna.

Table 2

Relative proportions of orders. % of whole population		Relative proportions of species within orders. % of order populations	
Collembola	58·9	*Pseudachorutes subcrassus*	96·5
		Other Collembola	3·5
Acarina	34·6	*Asca aphidioides*	24·6
		Hypochthonius pallidulus	24·4
		Other Acarina	51·0
Thysanoptera	4·7		
Other species	1·8		

From this table it is evident that the Collembola and Acarina show a marked predominance. Further, within these groups, 3 species are again predominant. *Pseudachorutes subcrassus* forms 96·5 % of a population made up of 8 species of Collembola; while in the mite fauna, of approximately 26 species, two of them together form nearly half of it. The "other species" constituting 1·8 % of the whole population are those larger species mentioned above. Not all are yet named, but there are probably about 40 of them. There are 2 species of thrips, one of which occurs only rarely.

The following is a list of the tussock population excluding the 1·8 % of larger species.

INSECTA
- COLLEMBOLA
  - Hypogastruridae
    - *Pseudachorutes subcrassus* Tbg.
    - *Friesia mirabilis* Tbg.
  - Isotomidae
    - *Isotoma notabilis* Schffr.
    - *Folsomia quadrioculata* Tbg.
  - Entomobryidae
    - *Lepidocyrtus cyaneus* Tbg.
    - *Orchesella villosa* L.
    - *Entomobrya nivalis* L.
  - Sminthuridae
    - *Sminthurides schötti* Axe
- THYSANOPTERA
  - 2 spp. indet.

ARACHNIDA
- ACARINA
  - Sarcoptiformes
    - *Hypochthonius pallidulus* Koch.
    - *Leiosoma simile* Nic.
    - *Damaeus clavipes* Hermann.
    - *Notaspis lupilis* Hermann.
    - *Hoplophora ardua* Koch.
  - Sarcoptiformes (*cont.*)
    - *Hermannia bistriata* Nic.
    - *Oribata avenifera* Mich.
    - *O. alata* Hermann.
    - *O. clavipectinata* Mich.
    - *O. globula* Nic.
    - *O. lucasii* Nic.
    - *O. punctata* Nic.
    - *O. setosa* Koch.
  - Parasitiformes
    - *Parasitus kempersi* Oud.
    - *Parasitus* sp.
    - *Eulaelaps stabularis* Koch.
    - *Pergamasus crassipes* L.
    - *Uropoda minima* Kram.
    - *Asca aphidioides* Kram.
    - *Zercon triangularis* Koch.
    - *Uliphis halleri* Canestrini.
    - *Sevis* sp.
  - Trombidiformes
    - *Trombidium* sp.
    - *Cyta latirostris* Hermann.
    - *Ericynetes* sp.
    - *Erythraeus* sp.

In addition to the above species, which occur regularly in the samples, the following larger animals, which are not confined to the tussocks, are of interest as possible predators on the tussock fauna.

INSECTA
- COLEOPTERA
  - Staphylinidae
    - *Tachyporus hypnorum* F.
    - *Metopsia clypeata* Müll.
    - *Philonthus varius* Gyll.
    - *Myllaena brevicornis* Matth.
    - *Staphylinus cupreus* Ross.
    - *Xantholinus tricolor* F.

ARACHNIDA
- ARANEIDAE
  - Thomisidae
    - *Xysticus erraticus* Bl.
    - *X. cristatus* Clerk.
- ARGIOPIDAE
  - *Pachygnatha degeerii* Sund.
  - *Erigone dentipalpis* Wid.

The Staphylinid *Tachyporus hypnorum* F. is the predominant species among the smaller carnivores of the Brometum and is everywhere abundant.

5. Distribution of the fauna within tussocks

Inasmuch as individual tussocks may be divided into regions of differing structure and microclimate it is to be expected that there will be localizations of different elements in their fauna. A number of tussocks were sampled by means of the Berlese method in which the upper parts of the tussocks (B) were extracted separately from the lower regions. On six occasions the fauna of the upper region was very significantly less dense than that in the lower regions. The average density for the upper region (B) was $2{\cdot}06 \pm 0{\cdot}53$; for the lower levels (A and C) it was $20{\cdot}7 \pm 5{\cdot}02$ organisms per g. of dry grass. On two other occasions, however, which differed from the above in that the samples were collected during heavy rain, the upper region gave densities of 7·7 and 18·0 organisms per g. as against 17·7 and 15·0 per g. respectively in the lower levels. Such an upward migration has been observed on other days when rain was falling. Though all the species present may rarely be found in the upper parts of the tussocks it is noticeable that the thrips (Thysanoptera) and Trombidiform Acarina form here a larger percentage of the fauna than in the lower levels.

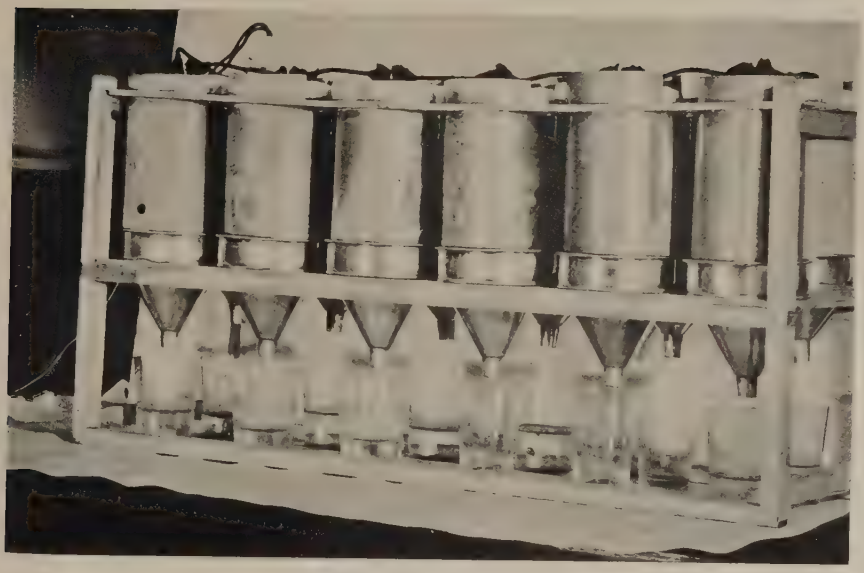
Further it will be seen from Tables 4 and 5 that there is a higher density for the fauna in the region of the living stock of the tussock than in the region of damp dead grass (C). The difference of the means of the total faunas in these tables is not, however, significant. The variability of samples from the dead grass region is considerably higher than that for samples from the living stock. Transpiration processes in the living tissue help to maintain a more constant moisture supply than is found in the dead material which is subject entirely to the drying power of the outer air. Thus, in the latter half of March, when the Brometum was beginning to dry up, the faunal densities in the two regions A and C do differ significantly, the mean of A between 15 and 20 March being $24{\cdot}5 \pm 2{\cdot}43$ and of C $9{\cdot}3 \pm 3{\cdot}36$.

In view of these results fluctuation data are now based on samples taken from the stock region of the tussocks (A) while additional check samples are taken from the two other regions.

6. Moisture requirements of Collembola

In the work of Maldwyn Davies (1928) it was suggested that contact with a film of water was necessary to Collembola in order that respiration in non-tracheate forms could be carried on through the skin. In the course of an unsuccessful attempt to maintain *Pseudachorutes subcrassus* alive on artificial media, observations on the manner of death under different conditions suggest another function of water in relation to the feeding of Collembola.

Two sets of four petri dishes were set up with a sterile agar jelly dissolved in a strong infusion of decaying *Bromus*. In one set 5% of cane sugar was



Phot. 3. Battery of 12 Tullgren funnels used for small samples.

Phot. 4. Components of the above.

added to the medium. 15 adult individuals of *P. subcrassus* were introduced into each dish. Temperature was not kept constant but all the dishes were subject to the same conditions. Since in all the dishes condensed moisture was abundant on the covers the saturation deficit in each case must have been almost nil.

In the four dishes without sugar all individuals became somewhat swollen and covered with drops of moisture within 24 hours. In 48 hours all were dead. There was a marked difference in the behaviour of the individuals on the 5% sugar medium. All were active after 24 hours, several having commenced to undergo ecdysis. After 48 hours 10% of them had died, showing a somewhat shrivelled appearance. Not until 5 days had elapsed were all dead and in no case had any "sweating" taken place.

The mouth parts of Collembola are of the biting type but are deeply withdrawn into the head, being enclosed by a kind of "box" formed by the labrum and labium. It is suggested that this "box" forms a sucking tube and that the biting mouth parts are used to abrade the surface of the food material which is then sucked in. In the first set of cultures death probably ensued from starvation, the sweated appearance suggesting that much moisture had been absorbed in the effort to obtain food. In the second set where food, in the form of sugar, was present, absence of sweating and continued existence suggest that the organisms were able to obtain nutriment without excessive absorption of moisture.

If, as the above experiment suggests, saprophagous organisms such as the Collembola feed by sucking moist food material, we have an explanation of the migration of these forms to and from different parts of the tussocks according to the variations in the moisture content. Thus the dead grass in the upper regions of the tussocks, when soaked by rain, becomes available as a food supply and likewise the dead grass in the lower less exposed parts ceases to be available as food when it dries up.

7. Fluctuations in the population

Having examined some of the environmental factors affecting the *Bromus* tussock populations it is now necessary to consider the variations in population density which occur during the winter.

The results obtained with the large samples extracted with a Berlese funnel are summarized in Table 3, in which population density is expressed as organisms per sq. m. of tussock grass. In Fig. 1 some of the data of this table are shown as smoothed curves $\left(\frac{a+b+c}{3}, \frac{b+c+d}{3} \text{ etc.}\right)$. Such smoothing has the effect of cancelling deviations not supported by previous and succeeding data. Adjustment is also made in similar fashion for unevenness of sampling dates. It will be noted that this smoothing removes from the graph the low figure for 14 December which is situated between peaks on 30 November and 29 December.

Table 3. *Density of tussock fauna. Large samples. Organisms per sq. m.*

Day and month	Collembola: *Pseudachorutes subcrassus*	Collembola: remaining spp.	*Asca aphidioides*	*Hypochthonius pallidulus*	Acarina: remaining spp.	Thysanoptera	Other species	Total: whole fauna
2. xi	5,184		352	16	1728	—	272	7,552
9. xi	3,792		400	560	1700	32	448	6,932
16. xi	2,736		256	1248	2176	128	576	7,120
30. xi	15,300		1600	3975	3981	1050	725	26,631
14. xii	6,614	200	480	2200	1400	424	208	11,526
29. xii	19,050	725	1625	1825	2712	325	200	26,462
5. i	9,625	300	1250	600	2375	425	225	14,800
13. i	7,000	350	825	675	1375	225	125	10,575
20. i	7,825	150	675	1000	1475	700	125	11,950
24. i	4,725	300	925	3275	1400	1275	275	12,175
28. i	5,662	212	1287	925	2208	962	111	11,367
1. ii	11,387	500	1825	2300	3871	961	85	20,929
5. ii	9,275	311	2787	1087	4012	647	149	18,270
9. ii	1,662	62	1262	400	2160	1024	86	6,656
14. ii	1,062	50	550	62	1172	400	86	3,382
20. ii	5,475	75	1425	250	1100	825	25	9,175
22. ii	4,636	349	1575	300	2885	412	498	10,655
24. ii	7,925	286	1087	150	2396	600	98	12,542
26. ii	9,687	212	762	1387	1921	612	149	14,730
1. iii	6,125	212	975	1662	2786	649	175	12,584
6. iii	3,962	61	375	175	571	499	73	5,716
9. iii	6,675	349	1425	562	3510	587	224	13,332
12. iii	4,187	162	375	200	1184	612	61	6,781
15. iii	4,525	149	500	225	1093	249	112	6,853
20. iii	4,950	75	325	137	697	324	61	6,569
15. iv	1,625	87	537	87	1012	162	150	3,660
Means	6,530	236	979	972	2034	543	205	11,497

During these months, in which a suitable technique was still being sought, samples were not taken with sufficient frequency to indicate more than a general increase of the population. For this reason some element of doubt must still remain regarding the population decline in January. On the data for February and March, however, more reliance may be placed.

During these months small check samples (Table 4) were also taken, as described above, within the tussock stock region A. These show curves (Fig. 2) essentially similar to those for the same period in Fig. 1; namely an increasing population in late January, followed by a sharp decline with low minima on 11 and 14 February, after which there is another increase followed by a decline in March.

The type of curve described and shown in Fig. 1 is most marked in the two predominant species, *Pseudachorutes subcrassus* and *Hypochthonius pallidulus* and to a somewhat lesser extent in *Asca aphidioides*, while it also characterizes the aggregate of remaining Acarina (Table 3, col. 5) and is thus imposed on the trend of the whole population (col. 8). It is not, however, evident in the trend of the Trombidiform mites, though these do not occur with sufficient frequency to warrant any conclusions being drawn concerning them. Likewise it is not shown by the Thysanoptera population nor by the species of spiders, beetles, etc. The trends of these latter populations are shown in Fig. 3.

It will be noted that the curve for the fauna excluding Collembola, Acarina and Thysanoptera shows a more or less steady decrease from the onset of

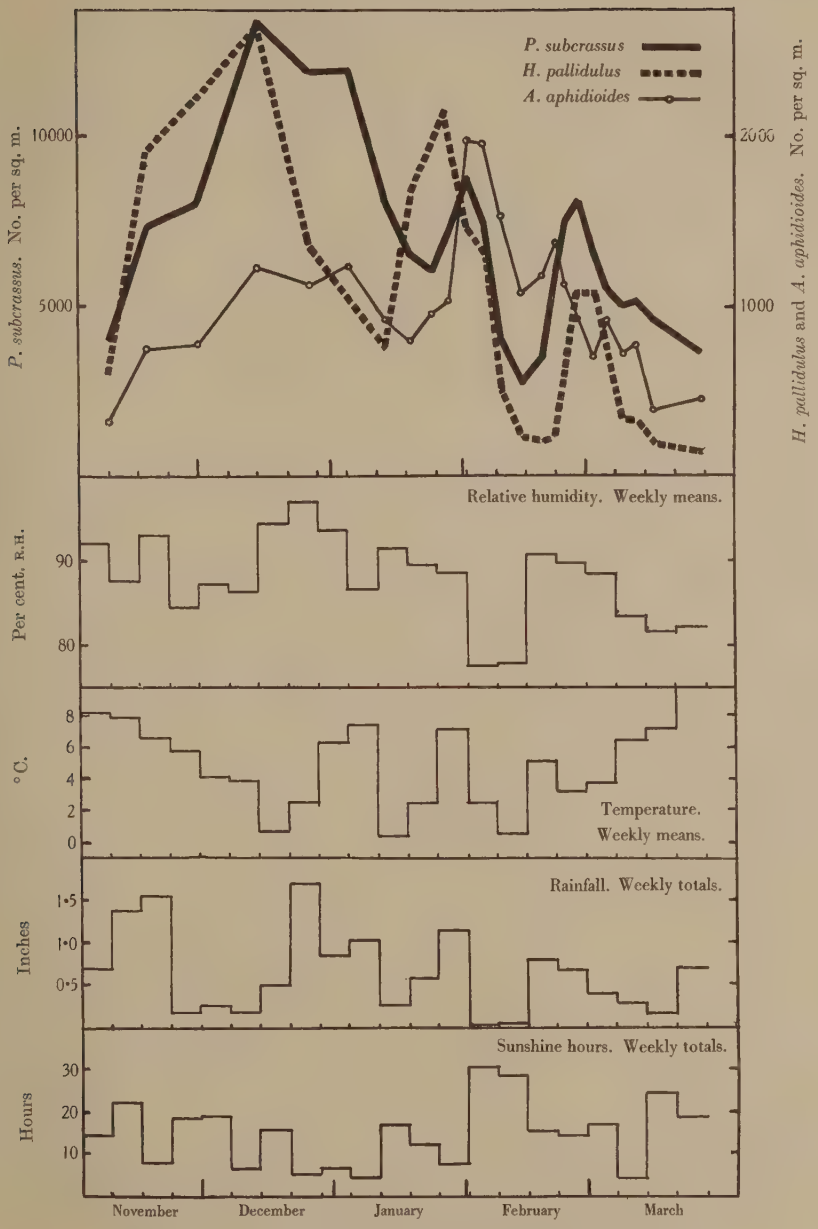


Fig. 1. Smoothed population trends of three species in the tussock fauna; with average weekly weather records

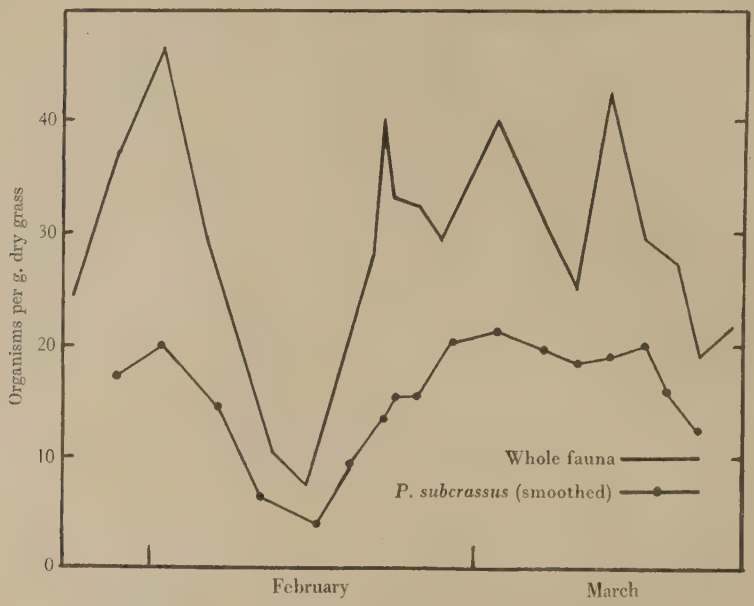


Fig. 2. Small sample curves for whole fauna (unsmoothed) and *P. subcrassus* (smoothed) in tussock region A.

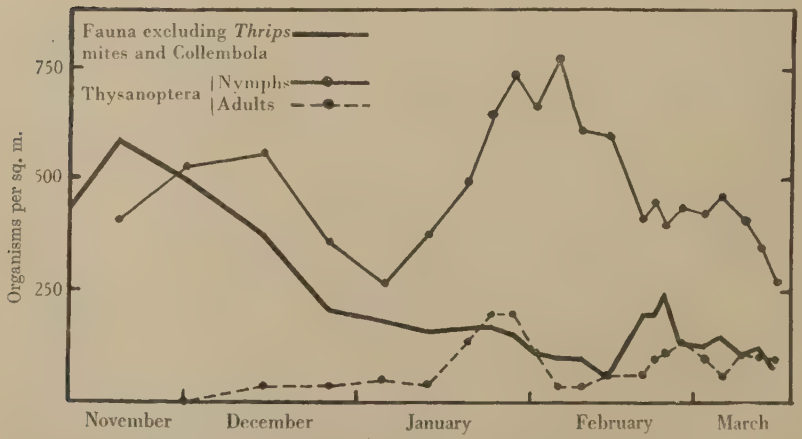


Fig. 3. Smoothed curve (large samples) for total fauna excluding Collembola, Acarina and Thysanoptera and curves for Thysanoptera, nymphs and adults.

Table 4. *Density of tussock fauna. Region A. Organisms per g. of dry grass*

Day and month	*Pseudachorutes subcrassus*	*Hypochthonius pallidulus*	*Asca aphidioides*	Total: whole fauna
24. i	10·0	6·0	1·8	24·4
28. i	17·8	6·7	3·2	37·2
1. ii	24·2	8·4	2·0	46·4
5. ii	18·0	1·2	4·8	29·6
11. ii	1·4	0·8	1·4	10·5
14. ii	0·6	0·4	0·4	7·7
20. ii	10·0	4·7	4·3	28·0
21. ii	18·6	3·9	1·6	40·0
22. ii	12·2	4·5	0·3	33·1
24. ii	16·6	1·0	6·0	32·4
26. ii	18·5	1·7	2·6	29·4
2. iii	26·1	2·2	2·7	40·0
6. iii	19·2	1·6	2·8	31·0
9. iii	14·3	0·8	2·9	25·2
12. iii	21·4	4·1	4·1	42·6
15. iii	20·1	1·2	1·7	29·7
18. iii	19·0	0·1	2·4	27·4
20. iii	9·7	0·3	2·4	19·2
23. iii	9·4	0·3	2·4	21·8
Means	15·1	2·6	2·6	29·2

Table 5. *Density of tussock fauna. Region C. Organisms per g. of dry grass*

Date and month	*Pseudachorutes subcrassus*	*Hypochthonius pallidulus*	*Asca aphidioides*	Total: whole fauna
1. ii	13·3	2·5	1·4	28·2
20. ii	21·6	2·6	1·6	35·3
22. ii	8·0	7·0	0·4	20·9
24. ii	8·0	0·8	0·4	15·5
26. ii	22·9	12·7	1·5	44·2
2. iii	6·4	2·0	1·1	17·0
6. iii	30·0	1·2	1·2	31·7
15. iii	0·4	0·7	1·2	4·7
18. iii	0·3	0·1	0·0	2·4
20. iii	5·9	3·0	0·9	14·6
23. iii	8·4	0·3	1·4	15·5
Means	11·3	3·0	1·0	20·9

sampling until the end of December, after which it maintains a fairly steady level. (The small peak in the latter part of February was due to the sudden appearance and disappearance subsequently of large numbers of Dipterous larvae of one species (22 February).) The initial decline of this population of larger species can be attributed partly to the death of species remaining over from the summer population and partly to the entrance into the soil for hibernation of other species, e.g. Isopods.

The majority of species represented in this curve, are, however, predatory and it is important to note that they do not fluctuate in any way which could account for the fluctuations in their prey, i.e. the Collembola and Acarina. The curve for Thysanoptera nymphs does, however, show fluctuations and it is possible that, although they do not exhibit the second decline, which, as will

be shown, can be attributed to environmental change, they do, nevertheless, show the characteristic bimodal form.

8. Discussion

It is not intended in this paper to discuss in detail the many possible causes of the fluctuations described. We may, however, examine the population decline which occurred in February. In addition to curves for populations, Fig. 3 represents graphically the main changes in weather. These records were obtained from the Radcliffe Observatory in Oxford and though they vary somewhat from the conditions at Headington they are sufficiently representative for the present purpose. It will be seen that the February minimum is coincident with a period of cold dry weather in which conditions were highly favourable to the drying out of the tussocks.

In addition to the data shown for this period it is necessary also to consider the direction of the wind. During the period under consideration the tussock structure was destroyed by strong east winds and the sheltering effect of the upper region of the tussocks, formed by the action of prevailing south-west winds, entirely removed. It is notable that the water content of the samples taken during this period was only 62% of their dry weight, as against an average of 149%. There is thus little doubt that a high evaporation rate was responsible for the February minimum. (In order to confirm that this minimum was due to death and not descent of the fauna into the soil, a mixed sample of soil, equal in area to one large grass sample, was washed out. The soil Collembolan *T. krausbaueri* was found and various mites in small numbers, but none of the tussock Collembola.)

It will be seen from examination of the weather data that there is no similar decrease in moisture content of the atmosphere which could account for the first decline in January. However, discussion of this fluctuation is reserved for a later publication, in which the present season's results will be reviewed.

9. Acknowledgments

I have to express my gratitude to many people who have materially assisted in this survey: Mr J. Hope-Simpson, School of Botany, Oxford, for describing the flora and physical features of the habitat; Dr J. R. Clapham, of the same School, for valuable advice on sampling methods; Mr J. M. Brown, Mrs M. Hughes, Commander J. J. Walker and Dr A. R. Jackson for naming Collembola, Acarina, Coleoptera and Araneidae respectively; Dr J. M. Walters, U.S. Dept. Agriculture, for assistance with the feeding experiment on *Pseudachorutes subcrassus*; Mr Charles Elton for his continued encouragement and finally Prof. G. D. Hale Carpenter for his generosity in allowing me to work in the Hope Department.

10. SUMMARY

1. Fluctuations occur in populations of saprophagous Collembola and mites during the winter. These fluctuations do not appear to be explained by environmental changes.

2. The present investigation concerns such a population inhabiting tussocks of the grass *Bromus erectus*. The general features of the habitat are described as well as the environmental features in the structure of *Bromus* tussocks which affect their fauna.

3. Samples were taken of whole tussocks and of parts of tussocks and the fauna extracted by a Berlese funnel and Tullgren funnels respectively.

4. The predominant groups present are the Collembola and Acarina. The Collembolan *Pseudachorutes subcrassus* is the most abundant species, the next in importance being two mites. *Hypochthonius pallidulus* and *Asca aphidioides*.

5. Moisture is of great importance for the existence of this fauna and the drying up or wetting of different regions of the tussocks causes migrations of certain species within them.

6. An experiment is described which suggests that abundant moisture in their food is essential to small saprophagous Arthropods since it would appear that their method of feeding is mainly suctorial.

7. A fluctuation of the population, with increases in November and December, early February and late February, with intervening minima, was shown to characterize the Collembola and Acarina (except possibly species of the Trombidiform group).

8. The February minimum was shown to correspond with a period of high evaporation rate, during which contrary winds destroyed the tussock structure. Discussion of other fluctuations is reserved for a later publication.

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THE OCCURRENCE OF DISEASE AMONG MUSKRATS (*ONDATRA ZIBETHICA*) IN GREAT BRITAIN DURING 1934

By TOM WARWICK

1. Introduction

Muskrat populations in Great Britain showed a marked decrease in the summer and autumn of 1934, mainly through the pressure of the Ministry of Agriculture and Fisheries' campaign. This period was an important turning point in the trend of numbers, and was followed by steady decrease to the present position of virtual extermination.

In the course of the ecological research programme carried out by the Bureau of Animal Population, Oxford University, under a grant from the Ministry, attention was given to natural mortality in muskrats. Any decrease observed might be due either to repressive measures or to such natural mortality: and it was important to distinguish between the two causes, in view of the confusion that has often arisen where voles, squirrels, rabbits and other animals have died out through natural epidemic disease and other causes, while control measures are actually in operation.

It should be said at once that in the present instance the main cause of the satisfactory decrease in muskrats in this country was undoubtedly the well-organized campaign of trapping. There were, however, several cases of disease just at the critical time in 1934, and there is a suggestion that the campaign may have been aided, to an extent unknown but probably rather small, by natural disease. This suggestion applies to Shropshire mainly, to Scotland possibly, but not to the South of England.

The pathological examinations were made by Dr G. M. Findlay at the Wellcome Bureau of Scientific Research, and I wish to thank him for permission to publish his findings, also Mr Charles Elton for help in preparing this report.

2. Normal health of muskrats

During the course of the muskrat investigations every animal dissected was carefully examined for disease. The great majority were healthy and in good condition:

Date	Number of muskrats examined (all localities)	Number found diseased
1933 Aug.	11	—
Sept.	27	—
Oct.	44	—
Nov.	67	—
Dec.	31	—
1934 Jan.	16	—
Feb.	39	—
Mar.	36	1
April	41	—
May	30	—
June	23	—
July	21	—
Aug.	19	1
Sept.	7	1
Oct.	1	—
Nov.	14	—
Dec.	4	—
1935 Jan.	3	—
Feb.	2	—
Mar.	1	—
April	2	—
May	1	—
	Total 440	
		Diseased 0·68 %

3. DISEASED MUSKRATS

(*a*) The diseased muskrat obtained in March in Shropshire had scattered foci of acute inflammation in the liver, caused by an early infection of the roundworm, *Hepaticola* (*Capillaria*) *hepatica*. Little of the liver tissue was affected and the animal was otherwise in quite good condition.

(*b*) On 24 August a dead muskrat was found in the Severn between Leaton and Rossall. A muskrat, presumably the same animal, had on 23 August been noticed on the river bank near the above spot in broad daylight. This muskrat proved on examination to have extensive lung disease. Both lungs were involved and very little healthy tissue was present in the left one, which had a large abscess. There were many adhesions between the lungs and the diaphragm, pleura, and pericardium. The animal, an adult female, was very thin, the flesh dark in colour and the fur sparse and loose.

(*c*) Out of seven muskrats from Shropshire in September only one was adult (a male) and this was trapped on the Severn at Pentre Island on the 24th. This individual had apparently been in the vicinity for some weeks before capture. On dissection it proved to have small scattered abscesses of the lungs which appeared as yellowish nodules present throughout both lungs; little of the tissue was affected. No adhesions were present nor was the animal emaciated. Two organisms were present in the lung and blood, a Gram-positive coccus and a Gram-negative bacillus. A portion of lung tissue was ground up in saline and filtered through a Berkefeld filter, the filtrate being inoculated intraperitoneally into mice, rats, guinea-pigs and rabbits. These animals remained quite healthy. Unfiltered material inoculated into the same

species intraperitoneally killed mice in 24 hours. From the mice was obtained a culture of a Gram-positive coccus, and a Gram-negative coliform organism which seemed to correspond in its fermentation reaction to *Bacillus cloacae*. Possibly the Gram-negative bacillus was only a faecal contaminant. The Gram-positive coccus, which was a haemolytic streptococcus, was more probably the actual cause of illness. It was highly pathogenic for white mice on intraperitoneal injection, and from seral and biochemical observations is related to other streptococci of animal origin.

(*d*) Unfortunately it was not possible to say what kind of organism was responsible in the first case found in August; but it seems, from the lesions encountered, not unlikely that the type of infection was the same in both muskrats. The two animals with diseased lungs were found when muskrat density had become rather low. It is unlikely in the sparse population that carcases of dying animals would be found frequently. The muskrats were obtained nearly 16 miles by river away from one another, and the one at Pentre was apparently an isolated individual occurring $4\frac{1}{2}$ miles above the length of river still more or less infested in 1934. The mortality may therefore have been fairly widespread.

(*e*) A muskrat with disease of the spleen was obtained in Scotland at Loch-an-Erie Pond, Gleneagles, in November 1934. Acid-fast bacilli were found, and these produced in two guinea-pigs lesions indicating a tubercular infection. The organism was of the bovine type.

4. Summary

Between August 1933 and September 1934, three out of 412 muskrats examined in Shropshire were found diseased. One (March 1934) had a diseased liver due to roundworms. The other two (August and September 1934) had lung disease, which in one case at any rate was associated with a pathogenic haemolytic streptococcus. One case of disease was also met with in Scotland (November 1934); this animal had a tubercular spleen.

It is suggested that natural disease may have assisted, to a small extent, the downward trend in muskrat numbers in the summer and autumn of 1934, due mainly to the trapping campaign.

THE FRESH AND BRACKISH WATERS OF BARDSEY ISLAND (NORTH WALES): A CHEMICAL AND FAUNISTIC SURVEY

By K. A. PYEFINCH

(*University College, Nottingham*)

(*With 4 Figures in the Text*)

CONTENTS

PAGE

1. Introduction 115
2. General account of the fresh water 115
3. The chemical analysis 119
4. The fauna 127
   (*a*) The fauna of the ponds 127
   (*b*) The fauna of the pools 130
5. The distribution and habitat of *Procerodes* (*Gunda*) *ulvae* . . 130
6. Acknowledgements 136
7. Summary 137
   References 137

1. Introduction

This paper is a record of collections and analyses made on Bardsey Island during three visits in 1935. It is hoped that the results will serve a double purpose: first, as a step in the proposed ecological survey of the island, and secondly, as an attempt to assess the rigour and changes in the environment of fresh-water animals living in small, isolated and sometimes ephemeral ponds.

Practically nothing is known about the fresh-water fauna of the island, such information as is available being in the form of scattered notes, contributed by investigators working on other problems (e.g. Coward (**6**)). Scott, however, when visiting the island in 1902 to collect lobsters, made a small collection of animals from one of the ponds. An account of this has recently been published (**14**), and his description of the pond makes it probable that it represents Pond 5 of the present survey. Beyond these records nothing is known.

2. General account of the fresh water

As indicated in a previous paper (**9**) and as shown by the sketch-map (Fig. 1) the fresh water of the island, though quite considerable in amount, is very scattered. There is a series of small, isolated ponds scattered chiefly over

the boulder clay area. These may be grouped roughly according to the source of their water as follows:

(*a*) Source of water entirely underground. The spring type.
(*b*) Source of water entirely land drainage.
(*c*) Source of water partly underground and partly land drainage.

Fig. 1. Sketch-map showing the distribution of fresh water, 1935.

The spring type of pond occurs along both sides of the mountain, though commoner on the western side. The most important ponds of this type lie in a line running roughly parallel with the long axis of the island, at the junction of the slate and boulder clay on the western side of the mountain. These springs are chiefly used as a supply of drinking water for the farms. They offer the most constant type of environment. The second type consists of shallow ponds found on the boulder clay. Ponds of this type are common and, as might be

expected, are the most ephemeral, many drying up altogether before the end of the summer. Environmental change is here at its maximum. The third type shows a wide range in the general rigour of the environment according to the local conditions and the seasonal changes also show considerable variation from one pond to another.

There is practically no permanent running water on the island. Small streams arise from many of the springs and run for a short distance along the bottom of the earthen banks, and in wet weather several small streams drain down the low cliffs along the western coast, but these are temporary in nature and have no permanent channels. The only permanent stream runs roughly from north to south along the middle of the cultivated boulder clay plain, draining a series of marshy areas. It runs into the sea on the western coast just north of Porth Solfach. Even in this stream the volume of water was much reduced later in the year.

From these scattered ponds and springs eight were so chosen that the full range of environment was adequately represented. Collections and analyses were made from these at each visit—in April, July and September. Their physical characteristics are summarized in Tables 1 and 2. As the outline of the ponds was, in many cases, irregular, the area given in Table 2 is only approximate. The measurements are intended merely to give some idea of the rate at which the various ponds were drying up.

Table 1

Pond No.	Position	Geology	Source of water	Type of bottom	Extent of shading	Pollution
1	Mountain, behind chapel	Slate	Underground	Rock, with a thin layer of mud	Half underground, deep shade	None
2	North-west of Nan't	Boulder clay	Land drainage	Mud	None	Considerable
3	West of Careg	Boulder clay	Spring water flowing over fields	Sand, some mud and stones	None	Considerable
4	West coast, a little north of Careg	Boulder clay	Underground and land drainage	Thick, foul mud	Slight, pond lies in a depression	Moderate
5	East of Lighthouse	Boulder clay	Underground and land drainage	Mud and stones	None	Slight
6	North of Porth Solfach, on coast	Boulder clay	Land drainage	Stones covered with mud	Slight	Moderate
7	West of Plas Bach	Boulder clay	Land drainage	Yellow, soft mud	None	Slight
8	North-west of Nan't, on sea coast	Boulder clay	Land drainage	Stones covered with mud	Slight	Slight

Table 2

Pond No.		1	2	3	4	5	6	7	8
Physical characters:									
Area (in ft.)	Maximal	1·6 × 2·1	12 × 96	36 × 9	30 × 3	15 × 9	3 × 6	30 × 27	4 × 3·5
	April	1·6 × 2·1	12 × 96	36 × 9	30 × 3	15 × 9	3 × 6	30 × 27	4 × 3·5
	July	1·6 × 2·1	9 × 72	33 × 9	24 × 3	15 × 9	3 × 5	—	4 × 3·5
	September	1·6 × 1·2	9 × 63	17 × 8	4 × 1·5	—	3 × 5	·	4 × 3·0
Depth (in ft.)	April	0·6	1–2	1–2	0·75	1·5	2·0	1–2	1–1·5
	July	0·6	1–2	1–2	0·5–1·0	1·0	1·0	—	0·5–1·0
	September	0·6	1	1	0·25	—	1·0	—	0·5–1·0
Condition of water	April	Clear, colourless	Turbid, yellowish brown	Clear, colourless	Suspended particles	Clear, colourless	Clear, colourless	Clear, colourless	Clear, colourless
	July	Clear, colourless	Turbid, yellowish green	Turbid, yellowish green	Suspended particles	Clear, faintly yellow	Clear, colourless	—	Clear, colourless
	September	Clear, colourless	Strongly turbid, deep green	Turbid, deep green	—	—	Clear, colourless	—	Clear, faintly green
Temperature (° C.)	April	8·8	9·7	11·1	12·2	8·8	8·6	9·4	11·6
	July	13·6	24·4	27·2	18·0	21·0	21·1	—	21·1
	September	14·3	14·1	19·4	—	—	15·2	—	15·5

3. The chemical analysis

The following observations were made in each case:

1. *Temperature.*

2. *Hydrogen-ion concentration.* This was determined in the field, by direct comparison with standard solutions. 10 c.c. of pond water were taken and 0·5 c.c. of indicator were added. For the standard solutions the following buffer mixtures were used:

Clark and Lubs KH_2PO_4-NaOH buffer	*p*H range 6·4–7·6
Sørensen's phosphate buffer (KH_2PO_4-Na_2HPO_4)	*p*H range 7·6–8·0
Clark and Lubs boric acid-KCl-NaOH buffer	*p*H range 8·0–8·6

The indicators used were brom-thymol-blue (*p*H 6·4–7·6) and cresol red (*p*H 7·6–8·6).

3. *Alkali reserve.* This was determined as soon as possible after the sample was taken. 10 c.c. of pond water were titrated against $N/100$ H_2SO_4, using methyl orange as indicator.

4. *Oxygen.* This was determined by Winkler's method. The first stage was completed within 3 hours of taking the sample, and the final titration against $N/100$ sodium thiosulphate carried out as soon as possible after returning to the mainland. The remaining salts were all determined after returning to the mainland.

5. *Silicates.* Atkins' modification of Dienert and Wandenbulcke's method was used (**2**).

6. *Phosphates.* Atkins' modification of Denigès' method (**1**). Where any appreciable amount of H_2S was present, addition of ammonium molybdate solution, either alone, as in the silicate analysis, or with sulphuric acid in Denigès' reagent in the analysis of phosphates, caused the development of a blue coloration due to molybdenum sulphide. Before estimating these constituents, therefore, the water was aerated for a short time. A period of aeration of 5 min. was found sufficient to remove all traces of H_2S.

7. *Chlorides.* These were determined by Mohr's method, by titrating with standard silver nitrate solution. Care was taken to adjust the *p*H of the solution so that it fell within the limits of 6·5–7·5. Outside this range the end-point tended to be indefinite when dilute solutions were used.

8. *Calcium.* This was precipitated as calcium oxalate, redissolved in sulphuric acid, and the resulting oxalic acid titrated against standard potassium permanganate.

9. *Magnesium.* This was precipitated as magnesium ammonium phosphate and the turbidity of the sample solution compared with that produced by a standard solution of magnesium sulphate.

The concentrations of ammonia and of nitrates were also determined, but

the results obtained were so variable as to suggest that further work is necessary before satisfactory generalizations can be made for ponds of this type.

Milk bottles of green glass, with a porcelain stopper with a rubber ring and clamped on by a clip were used for all the samples. The sample bottles used had been in use previously for this type of work. Care was taken to fill all the bottles full when taking a sample, so as to minimize changes due to gaseous exchange.

Discussion of results: introduction and general considerations

As has been indicated already, the eight ponds selected present a considerable variety of environment. The controlling factors of this environment are numerous and their interaction complex. In an investigation of this type, it is doubtful whether any satisfactory and complete analysis could be made of these factors, even if the chemical analyses were prolonged over a much longer period than that surveyed in the present study. Thus it was thought better to present the chemical results as they are, as an indication of the type and magnitude of the variations possible in this specialized environment, rather than to attempt any complete analysis of these factors. The controlling factors may, however, be broadly summarized as follows:

1. *Source of water.* This may be:
   - (*a*) Underground (spring water).
   - (*b*) Land drainage.
   - (*c*) A combination of (*a*) and (*b*) in varying degrees.
2. *Degree of exposure.* This affects:
   - (*a*) Temperature range.
   - (*b*) The rate of evaporation—most rigorous in isolated, shallow ponds included under 1 (*b*).
3. *Type of bottom.* There were three types:
   - (*a*) Solid rock, usually with a thin layer of mud.
   - (*b*) Large stones with mud.
   - (*c*) A thick layer of mud, in every case overlying rock below.

Generally speaking, the nature of the bottom affects the fauna more than the chemical environment, but in cases where the mud was foul and sulphurous (e.g. pond 4) there was a profound effect on the concentration of oxygen.

4. *Situation.* The action of this factor may be considered in three ways:
   - (i) As affecting the degree of pollution.
     - (*a*) None or very slight in the spring type of pond, which was usually protected.
     - (*b*) Moderate to slight in the outlying ponds.
     - (*c*) Considerable in the large, shallow ponds near the farms, where the source of water was land drainage.
   - (ii) The effects of the geology of the subsoil.

(iii) The proximity to the coast. The effects of sea spray were usually marked. Their effect varied with:

(*a*) Distance from the coast.

(*b*) Configuration and type of coast near the pond.

(*c*) Position of the pond. The effects of spray varied with the position of the pond on the coast. This variation was probably due to differences in the prevailing winds.

General climatic conditions

An analysis, made of the records of rainfall and sunshine for Holyhead (the point nearest to Bardsey where such records are kept), shows that the amount of both rainfall and sunshine was rather greater than the average, but not abnormally so. The actual figures are:

Table 3

	Rainfall (in mm.)			Sunshine (in hours)		
Period	Actual	Average	Diff.	Actual	Average	Diff.
October–March, 1934–5	587	515	+72	380	436	−56
April–September, 1935	385	373	+12	1205	1099	+106

Detailed discussion of results

1. *Temperature* (Table 2). The spring type of pond (pond 1) showed least seasonal variation; the shallow, exposed ponds (ponds 2 and 3) the greatest variation, and the other ponds intermediate ranges. Observations of the diurnal range (made in September) show a similar grouping, varying from a range of 14·1 to 18·1° C. for pond 3, to 13·7 to 14·3° C. for pond 1, a spring type in deep shade.

2. *Hydrogen-ion concentration* (Table 4). The variation of *p*H from one pond to another was greatest in April, when it varied from *p*H 6·4 (pond 5) to *p*H 8·45 (pond 2), and least in September, when the range was from *p*H 7·4 (pond 8) to *p*H 6·8 (ponds 1 and 3). In general, there was an increase in acidity during the season, this tendency being most marked in pond 2. From all points of view this type of pond presents the most variable type of environment. From measurements made in September, diurnal variations in *p*H were found to be slight. In all the ponds investigated in this way vegetation was scanty or absent, so that little diurnal change was to be expected.

Table 4. *Hydrogen-ion concentration*

Pond No.	April	July	September
1	6·6	6·7	6·8
2	8·45	7·4	6·9
3	7·5	7·3	6·8
4	7·3	6·9	6·9
5	6·4	6·4	—
6	7·6	7·6	7·2
7	7·5	—	—
8	8·0	7·3	7·4

It does not seem possible to interpret the effects of evaporation and decreasing quantity of water on the hydrogen-ion concentration except in terms of a complete knowledge of the chemical conditions and their variation. Welch (**16**, p. 337) records some cases where there are progressive changes in *p*H during drying and others where little change takes place. During the September visit, pond 3 was drying rapidly, but this did not involve any significant changes in *p*H (the variation was between *p*H 6·8 and 7·0). As will be shown later, this comparatively constant *p*H value masked important and radical changes in the concentrations of the salts present.

3. *Alkali reserve* (Table 5). The general decrease in the values of *p*H was accompanied, on the whole, by an increase in the alkali reserve. The only exception to this was pond 8, where the September readings showed an increase in alkali reserve (0·0050–0·0071 *N*) together with a slight increase in *p*H (7·3–7·4). A noticeable feature is the great increase in the alkali reserve of pond 3 for September, an increase probably connected with the rapid drying of this pond.

Table 5. *Alkali reserve*

All results expressed in terms of normality

Pond No.	April	July	September
1	0·0032	0·0023	0·0019
2	0·0037	0·0040	0·0049
3	0·0030	0·0030	0·011
4	0·0054	0·0058	—
5	0·0012	0·0016	—
6	0·0037	0·0040	0·0048
7	0·0042	—	—
8	0·0038	0·0050	0·0071

4. *Oxygen* (Table 6). The results are expressed both as concentrations of oxygen (c.c. O_2/l.) and as percentage saturations. The saturation values are taken from Seidel's tables.

Table 6. *Oxygen*

The results are expressed both as concentration of oxygen (c.c. O_2/l.) and also in terms of percentage saturation

	April		July		September	
Pond No.	Conc.	% Satn.	Conc.	% Satn.	Conc.	% Satn.
1	3·99	49·1	4·73	65·1	4·12	57·5
2	4·73	59·1	6·08	104·1	1·94	27·0
3	4·31	56·1	9·84	177·7	0·34	5·25
4	2·23	29·7	4·21	63·6	—	—
5	4·74	58·4	0·00	00·0	—	—
6	3·97	48·6	3·91	62·8	2·40	34·34
7	3·88	48·6	—	—	—	—
8	3·76	49·3	3·40	54·6	4·70	67·5

In April the ponds fell roughly into three groups:

(*a*) Those with 56–60 % saturation. Ponds 2, 3 and 5. All are shallow exposed ponds, ponds 2 and 3 being particularly so.

(*b*) Those with 48–50 % saturation. Ponds 1, 6 and 8. All are in moderate or rather deep shade.

(*c*) Those with 30 % saturation. Pond 4. This low value is probably due to the thick layer of sulphurous mud forming the bottom of this pond.

Ponds 2 and 3 showed, as might be expected, the greatest variations during the season. In July both were supersaturated (pond 2 104 % and pond 3 177 % saturation). The oxygen readings in both cases were taken during the afternoon (3.40 and 3.50 p.m. respectively) so that some degree of supersaturation was likely. The figure for pond 3 is comparable with that found by Butcher *et al.* (**4**) for river water. Pond 3 showed a rapid fall in the autumn to the low value of 5·2 % saturation.

Of the remaining ponds, pond 1 showed the most constant conditions and the results for pond 6 were rather similar. Pond 8 showed a steady rise throughout the season. The reason for this is not easy to suggest but this pond was anomalous in other respects also. Finally, pond 5 showed complete absence of oxygen in July. This condition may have been purely temporary, but it may also have been the prelude to complete drying, as there were indications from the other ponds (e.g. ponds 2, 3 and 6) that the period of drying was marked by a rapidly decreasing concentration of oxygen. Also, much of the bottom of pond 5 was covered with a thick layer of mud.

5. *Silicates* (Table 7). Little is known in detail about the variation in silica content of fresh waters, so that few comparable data are available. Pearsall(**12**) for the English lakes, found a vernal maximum in April. This was followed by a rapid decrease, a second maximum in July, then a decrease to September. Atkins & Harris (**3**), working on Staddon Reservoir and Borough Farm Pond, found that the silicate curve followed that for *p*H and therefore suggested that the amount of silicate depends upon the degree of alkalinity of the water: the greater the latter the greater the amount of silica dissolved. In most cases this cannot be wholly true, as, unless there is a large reserve of silicate, the demands of the flora and fauna must exert some effect.

Table 7. *Silicates*

All results expressed in terms of mg. SiO_2/l.

Pond No.	April	July	September
1	0·0	3·17	3·07
2	0·0	6·45	3·20
3	0·0	3·50	5·00
4	0·0	5·62	—
5	0·0	1·25	—
6	0·0	5·20	5·78
7	0·0	—	—
8	0·0	6·78	3·15

The results from the Bardsey ponds show indications of several of these factors. First, silica was absent in all the ponds in April, probably due to temporary exhaustion after the spring diatom maximum. Secondly, from April

to July there was a sharp increase in the concentration of silica. The steepness of the curves for this short period gives some idea of the rigour of the changes occurring in these small ponds. To some extent, the amount of silica in July corresponds to the reaction of the water; thus the most acid ponds (5 and 1) show the least silicate and the more alkaline (pond 2) show more silicate. There is only a partial correlation, however, as the silicate concentrations do not exactly follow the *p*H values.

Finally, the general tendency from July to September seems to be for a decrease in the silicate concentration, though ponds 3 and 6 show increases. This increase in the case of pond 3 is probably due again to the drying of this pond, but the explanation of a similar increase in pond 6 is not obvious. Pond 1 showed only a very slight decrease, it is just possible that this may be due to the increasing alkalinity of this pond.

6. *Phosphates* (Table 8). Other work on the phosphate cycle in fresh waters (Pearsall (**12**) for the English Lakes; Atkins & Harris (**3**); and unpublished observations of the writer) indicates that the main features of this cycle are an early maximum (March: Pearsall, Atkins & Harris; February: Pyefinch), a much lower maximum in midsummer and low and rather variable amounts of phosphate until late in the year. The period for which observations of the Bardsey ponds were made thus coincides with that during which there are no striking changes. With two important exceptions, all the ponds show small and unimportant changes. The exceptions occur in ponds 2 and 3. Pond 2 showed a very high concentration of phosphate in April (1·66 mg. P_2O_5/l.) and, though there was a considerable drop to July, the phosphate remained high throughout the year. Pond 2 is situated close to a farm, so that this difference may safely be attributed to local conditions. Pond 3 was normal, or practically so, until September when a value of 0·5 mg./l. was recorded. As before, this was probably due to drying.

Table 8. *Phosphates*

All results are expressed in terms of mg. P_2O_5/l.

Pond No.	April	July	September
1	0·027	0·012	0·009
2	1·66	0·227	0·270
3	0·013	0·090	0·50
4	0·024	0·030	—
5	0·021	Trace	—
6	0·024	0·035	0·022
7	0·010	—	—
8	0·016	0·016	0·012

7. *Chlorides* (Table 9). The amount of sea spray seems to be the most potent factor in determining the concentration of chlorides. The ponds fall into two groups: first, ponds 4, 5 and 8, and second, ponds 1, 2, 3, 6 and 7. The ponds in the first group are all situated on or near the sea shore. Pond 5, with the highest concentration of chloride, is situated at the head of a long, funnel-shaped gully containing large boulders and near a rocky, exposed part of the

shore. Pond 4, with less chloride, is situated on the low cliffs of the western coast but is rather more sheltered. Pond 8, though near the coast, is much more sheltered and shows still less chloride.

Table 9. *Chlorides*

All results are expressed in terms of g. Cl_2/l.

Pond No.	April	July	September
1	0·065	0·075	0·062
2	0·089	0·131	0·218
3	0·084	0·086	0·274
4	0·347	0·400	—
5	0·521	0·868	—
6	0·114	0·127	0·145
7	0·114	—	—
8	0·174	0·344	0·405

Of the ponds of the second group, ponds 1, 2 and 3 are all inland, but pond 6 is on the seashore. The low chloride concentration seems to be due to the effects of a small stream which flows through it. This suggestion is supported by the readings taken of small rock pools on the shore below where, as is shown in the table below, the concentration of chloride entirely depends upon their proximity to the stream.

Table 10. *Concentration of chlorides in rock pools below pond* 6

Pond or pool	Chloride g. Cl_2/l.	Description and position
Pond 6	0·114	(See Map)
Pool 5	0·114	Immediately below cliff, well above high-water springs. Stream flowing through
Stream over stones	0·176	Just below high-water springs
Pool 7	2·074	Below high-water neaps, and off the main stream
Pool 8	0·316	Below high-water neaps, but with stream flowing through

As regards their seasonal variations, all the ponds of the first group show an increase in the amount of chloride. Unfortunately, only one, pond 8, persisted throughout the season. Of the landward ponds, pond 1 is again the least variable, with practically a constant concentration of chloride, ponds 2 and 3 both show some increase, the latter is particularly marked in the case of pond 3. This increase can safely be attributed to the concentration of solutes due to drying.

Pond 6 also showed little variation, except for a slight increase between July and September. This is rather remarkable, as during this period the stream feeding the pond had been dammed further up to form a drinking place for sheep and cattle. Thus it seemed likely that the chloride should increase considerably. The explanation probably may be attributed to two factors:

(*a*) The pond is sheltered from the sea spray to some extent, as it lies below the level of the cliff.

(*b*) It is situated opposite a part of the shore which is itself sheltered. Moreover, an analysis of the prevailing wind frequencies at Holyhead shows that there were few high winds from the south or south-west between July and the time of analysis in September. As these are the only winds which would cause much spray at this point, a more constant chloride content is more likely.

8. *Calcium* (Table 11). As Ritchie (**13**) has pointed out, the concentration of calcium in fresh waters is very variable, and is dependent upon a number of factors (e.g. amount of rainfall, treatment of surrounding soil, drainage basin, etc.) the effects of which are not very easy to assess. The figures show that the Bardsey ponds have a tremendous variation in calcium content, both from one pond to another and also through the season, e.g. ranging from 29·0 mg. Ca/l. for pond 1 to 77·0 mg. Ca/l. for pond 4, and with seasonal variations ranging from 9·25 mg. Ca/l. for pond 1 to 38·0 mg. Ca/l. for pond 8. There is nevertheless, a rough correlation between the calcium content and the alkali reserve readings. For example, pond 4, in April has the highest alkali reserve and the highest calcium content; an increase in alkali reserve between April and July is accompanied by a rise in the concentration of calcium. Again, ponds 1 and 5, with low calcium contents, have low values for the alkali reserve. This correlation is only partial, however, and breaks down for the inland ponds (2 and 3), where the influence of the other factors mentioned above would be greater.

Table 11. *Calcium*

All results are expressed in terms of mg. Ca/l.

Pond No.	April	July	September
1	29·0	28·75	19·75
2	33·25	37·25	32·5
3	36·25	28·25	53·5
4	77·0	85·5	—
5	22·75	31·5	—
6	42·5	50·75	60·5
7	45·0	—	—
8	44·0	74·0	82·5

9. *Magnesium* (Table 12). The variations in the magnesium content of fresh waters must be correlated with the flora and its demands upon magnesium for chlorophyll formation. Unpublished observations of the author on this question show that the main features of the magnesium cycle are a decrease in the early spring (presumably due to increased chlorophyll formation of the growing plants and the developing phytoplankton), followed by a steady increase during the rest of the year. The results for the Bardsey ponds fall into line with these observations, though the rate of increase in the magnesium content is noticeably faster than in a larger body of water. It is interesting to note that the results fall into two groups: first, ponds 4, 5, 6 and 8 where the vegetation was abundant, and second, ponds 1, 2 and 3 where the vegetation

was scanty. The decrease in pond 6, observed in September, seems quite anomalous, and there does not seem to be any obvious explanation.

Table 12. *Magnesium*

All results are expressed in terms of mg. Mg/l.

Pond No.	April	July	September
1	3·55	4·94	5·29
2	3·55	6·64	7·94
3	4·07	6·01	7·80
4	5·34	9·78	—
5	6·30	9·89	—
6	5·54	8·72	7·29
7	4·45	—	—
8	5·24	8·72	10·35

In all cases a dash (—) in the readings indicates that the pond had dried up at that stage.

4. THE FAUNA

(*a*) *The fauna of the ponds*

The collections made in the various ponds are summarized in the table below (Table 13). Only the larger forms are listed in this table, as the collection of the smaller forms (particularly small Crustacea) cannot be said to be representative. This deficiency is partly due to the difficulty of using plankton nets in small, shallow ponds of the type found on the island and partly because it was not possible to visit the island at the times when the Entomostraca were likely to be most abundant. The following is the list of the species of Entomostraca which were collected:

Cladocera.	*Chydorus sphaericus* (O. F. Müller)
	Simocephalus vetulus Schrödler
Ostracoda.	*Cypria ophthalmica* (Jurine)
	Herpetocypris reptans (Baird)
Copepoda.	*Cyclops viridis* (Jurine)

In addition to these Scott (**14**) has recorded:

Cladocera.	*Chydorus barbatus* G. S. Brady
	Alona tenuicaudis G. O. Sars
Ostracoda.	*Eucypris virens* (Jurine)
	Cypridopsella villosa (Jurine)
	Candona lactea (Baird)
	C. candida (O. F. Müller)
	Ilyocypris biplicata (Koch)
Copepoda.	*Leptocyclops agilis* (Koch)
	Platycyclops fimbriatus Fischer
	Dactylopusia brevicornis (Claus)
	Canthocamptus minutus Claus

The occurrence of *Dactylopusia brevicornis* in a fresh-water pond is interesting, as this species is normally a shore living form. The high chloride content of pond 5 (noted above) and the series of saline pools below this pond (see section (*b*) below) suggest an explanation of the occurrence of this species in this situation.

Table 13. *The fauna of the ponds*

Species	Pond 1	2	3	4	5	6	7	8
PLATYHELMINTHES								
TURBELLARIA								
Polycelis nigra (Ehrenb.)	*	×	×	×	×	×	×	×
Planaria sp. (?)	*	–	*	–	–	–	–	–
ANNELIDA								
OLIGOCHAETA								
Tubifex sp.	–	×	×	–	–	–	–	–
Limnodrilus sp.	–	×	–	×	–	–	×	–
HIRUDINEA								
Herpobdella octoculata L.	–	–	×	×	–	×	–	–
Helobdella stagnalis L.	–	×	–	×	–	×	–	×
Glossosiphonia complanata L.	–	–	–	–	–	×	–	–
ARTHROPODA								
CRUSTACEA								
Isopoda								
Asellus meridianus Rac.	*	×	×	×	–	×	×	×
Amphipoda								
Gammarus chevreuxi Sexton	–	–	–	×	×	×	–	×
INSECTA								
Hemiptera								
Macrocorixa Geoffroyi Leach	–	×	×	×	–	×	–	–
Sigara fabricii Fieb.	–	×	–	–	×	–	–	×
Gerris sp.	–	×	–	–	–	–	–	–
Trichoptera								
Limnophilid case	–	–	–	–	–	–	–	×
Coleoptera								
Hydroporus palustris L.	–	–	–	×	–	–	–	–
Haliplus nomax B.B.	–	–	–	–	×	–	–	–
H. lineaticollis Marsh	–	–	–	–	–	×	–	–
Diptera								
Tipulid larva	–	–	–	–	–	–	–	×
Simulium sp.	–	–	–	–	–	*	–	–
Chironomus sp. (*thummibathophilus* group)	–	×	–	–	–	–	–	–
Chironomus sp. (*plumosus* group)	–	×	–	–	–	–	–	–
Eutanytarsus sp. (*inermis* group)	–	–	–	–	×	×	–	–
Eristalis sp.	–	–	×	–	×	–	–	–
MOLLUSCA								
GASTEROPODA								
Limnaea peregra (Müller)	–	×	×	–	×	×	×	×
L. truncatula (Müller)	–	×	–	–	–	–	–	×
Planorbis spirorbis (L.)	–	×	–	×	×	–	×	×
Planorbis crista (L.)	–	–	–	×	–	–	–	–
LAMELLIBRANCHIATA								
Sphaerium lacustre (Müller)	–	×	–	–	–	–	–	–
Pisidium milium Held.	–	–	–	–	–	×	–	–
P. cinereum Alder	–	–	–	–	–	–	–	×
P. subtruncatum Malm.	–	–	–	–	–	–	–	×
CHORDATA								
VERTEBRATA								
Pisces								
Anguilla anguilla (L.)	–	–	–	–	–	×	–	–
Amphibia								
Molge palmata Boulenger	×	–	–	–	–	–	–	–

× indicates presence.
* present in the stream leading away from the pond, not actually present in the pond itself.
– indicates absence.

Notes on the fauna

Turbellaria. *Polycelis nigra* was the commonest species, occurring (often in some abundance) in all the ponds studied. Another small Triclad was found in the small stream leading into pond 1 and in the stream leading into pond 3. So far as can be made out from a study of its external features, it differs from all the British species yet described. A detailed investigation of this animal is being carried out to determine its real status. The estuarine species, *Procerodes* (*Gunda*) *ulvae*, occurred in several places on the island. Its ecology is discussed in detail below.

Annelida. The Oligochaetes, *Tubifex* and *Limnodrilus*, occurred wherever there was a thick layer of mud on the bottom of the pond. In some cases they were especially abundant: for example, the bottom of pond 4 in April seemed to be a writhing mass of *Limnodrilus*. Whitehead (**17**) has pointed out differences in the food of the three species of Hirudinea found on the island. *Herpobdella* feeds chiefly on Chironomids and Oligochaetes, whereas *Glossosiphonia* and *Helobdella* prey on Gasteropods. The distribution of these leeches on Bardsey bears out this statement, as in every case the preferred food was available.

Crustacea. *Asellus meridianus* was the only species of Isopod occurring on the island, the commoner *Asellus aquaticus* being completely absent. This dominance of *A. meridianus* is surprising, especially as there are wide differences in the calcium concentrations between the various ponds. The brackish water *Gammarus chevreuxi* was the only species of Amphipod to be found. It was confined to the ponds (4, 5, 6 and 8) near the seashore. No strictly freshwater species of Amphipod occurs on the island.

Insects. Generally speaking, very few species of aquatic insects were recorded, though in some cases large numbers of individuals occurred. For example, of the Hemipteron *Macrocorixa Geoffroyi* was particularly abundant in ponds 2 and 3 later in the year, when it became the dominant member of the fauna of these ponds.

The Diptera were the only other insect group to be represented in any numbers. Chironomid larvae occurred in several of the ponds and pools and were occasionally abundant (e.g. pond 5, pools 1, A). The "rat-tailed" larva of *Eristalis* was found in ponds 3 and 5 in July. This larva has been used as an indicator of low oxygen concentration (down to less than 20 % saturation) ((**5**), p. 232). Though its occurrence on Bardsey was not sufficiently wide to warrant any generalization, the presence of *Eristalis* was not necessarily an indication of low oxygen content as, though there was no oxygen in pond 5 in July, the water of pond 3 was supersaturated at this time. It was also found in September in a small pond formed by the blocking of the stream leading to pond 8, the oxygen content here was 2·27 c.c. O_2/l., or 32·5 % saturated.

Mollusca. *Limnaea peregra* and *Planorbis spirorbis* were by far the commonest species of Gasteropods. *Limnaea truncatula* was rare, only two specimens being collected during the surveys.

Vertebrates. The only fish found were small elvers (*Anguilla anguilla*) which occurred in pond 6. Eels seem to occur sporadically in many of the ponds, as they were found in pond 5 in 1933, and the islanders state that they have been known to occur in pond 2.

The only other vertebrate was a single specimen of the palmated newt (*Molge palmata*) which was seen in pond 1 in April. Newts have been recorded on the island for a considerable period (**6**, **7**, **10**), but no other Amphibia are known to occur. Anura are completely absent and there is a local tradition that frogs die when brought on to the island. More recently, attempts have been made to breed frogs but these have not been successful. The reason most generally put forward for the lack of Anura is the amount of sea spray always present in the air and the consequent high salinity of the fresh water. Though Amphibia are very susceptible to the amount of salt in the water (**8**, p. 72) this cannot be the only prohibitive factor on Bardsey, as some of the inland ponds have salinities lower than those at which frogs are known to be able to live and breed.

(*b*) *The fauna of the pools*

Two of the series of the pools stretching down to the seashore were investigated; one series (pools A–K) are described in some detail below. The other series were situated in the rocky gulley leading up from the seashore towards pond 5. This pond overflows over the edge of the cliff and down the gulley. As the flow of the fresh water down the gulley was very variable and different pools were cut off from the direct flow of fresh water according to the volume flowing down, these pools present a very varied environment. Only pool 4 was in regular connexion with the sea. At all times their salinity is high and after storms the latter may rise to that of sea water.

Pool 1 has a layer of mud, some 2 or 3 in. thick, on a rock basis, but the other pools have a bottom of loose stones. Under these circumstances, the fauna is naturally scanty. *Eutanytarsus* sp. occurred in numbers in the mud of pool 1, *Gammarus chevreuxi* was common in all and *Procerodes* (*Gunda*) *ulvae* occurred in pool 4. Occasionally marine species were to be found, e.g. *Ligia* sp. in pool 3.

5. The distribution and habitat of *Procerodes* (*Gunda*) *ulvae*

This planarian worm occurs in at least four places on Bardsey:

(*a*) In the estuarine region of the stream leading down from pond 8 to the sea.

(*b*) In a large, brackish-water pool near the northern end of the island on the western coast. The chloride content of this pool was 12·23 g. Cl_2/l., or roughly 62 % sea water in September.

(*c*) In pool 4 of the series of pools below pond 5. *Procerodes* was found here only in April, it had disappeared in July and in September. Here again conditions were estuarine.

(*d*) In a series of rock pools below pond 6.

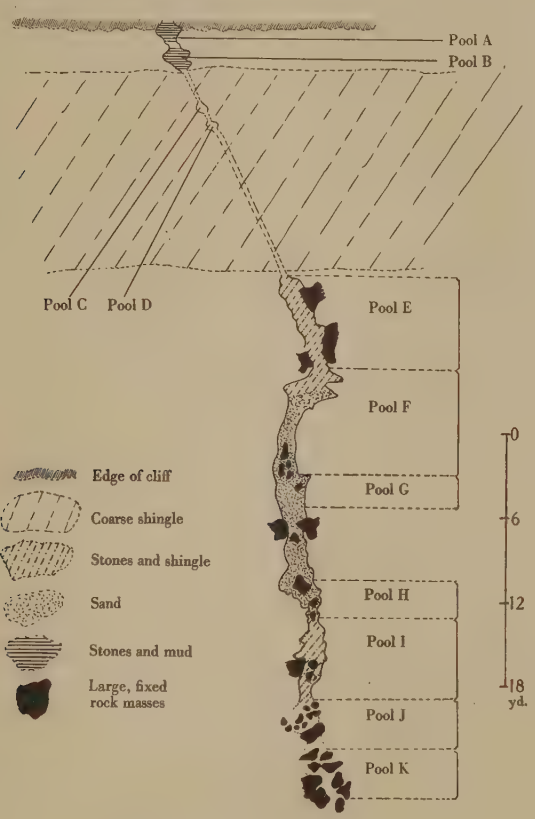

Fig. 2. Rock pools below pond 6.

The last case was examined in some detail. Topographically, it presents an almost exact parallel with the stream at Wembury as described by Pantin (**11**). An outline diagram of the pools is given in Fig. 2. The water from pond 6 falls over the low cliffs into two shallow pools (A, B), which run into one another. Below pool B is a stretch of coarse shingle, about 17 yd. across, shelving down to the rocky shore below. This corresponds to the "desert" area described by Pantin. After leaving pool B, the stream disappears in the shingle, except for two very small, ephemeral pools (C, D). Beyond the shingle the stream flows

through a series of rock pools (E–K). The high-water mark for spring tides occurs a little way below pool D (see Fig. 3).

The distribution of planarians in this series of ponds and pools was mapped out in detail. In the whole series only two species occurred: *Polycelis nigra* (Ehrenb.) and *Procerodes* (*Gunda*) *ulvae* (Oersted). In all cases, the planarians

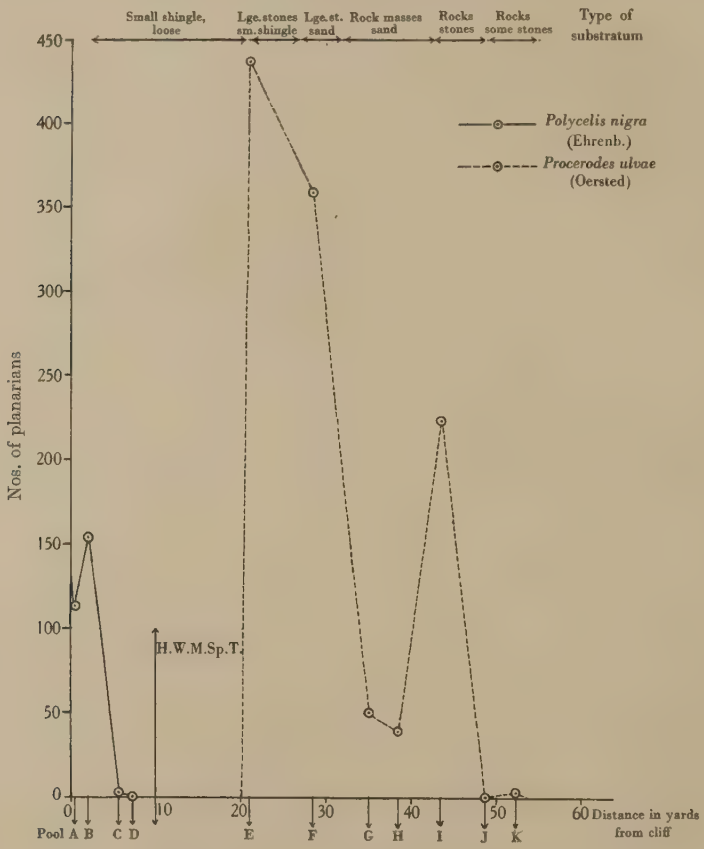

Fig. 3. Distribution of planarians. Stream system.

occurred under stones. No *Polycelis* could be found on the mud. This made an estimation of the populations of these planarians possible. A map of each pool was made and the position of each stone within the pool inserted. The numbers of planarians under each stone was then counted. This method gave a reasonably accurate estimate of the planarian population of each pool, except in one or two instances where small aggregations of young planarians occurred. Then

the count could only be made approximately, but these cases were too rare to affect the main results of this population study.

The populations, both of *Polycelis nigra* and of *Procerodes ulvae* are shown in Table 14, and the results expressed graphically in Fig. 3.

Table 14. *Populations of* Polycelis nigra *and* Procerodes ulvae

Pool	*Polycelis nigra*	*Procerodes ulvae*	Pool	*Polycelis nigra*	*Procerodes ulvae*
A	113	—	G	—	50
B	154	—	H	—	39
C	1	—	I	—	223
D	—	—	J	—	—
E	—	437	K	—	2
F	—	358			

Fig. 3 emphasizes the fact that *Polycelis* rapidly disappears above high-water mark of spring tides, whereas *Procerodes* appears equally suddenly just below this point. It also shows that a considerable variation in the numbers of *Procerodes* occurred from pool to pool. This variation seems to be connected with the type of substratum. In pools E and F, where it was particularly abundant, the substratum consisted of moderate-sized stones resting on shingle, though towards the bottom of pool F this shingle was being replaced by sand. The substratum in pools G and H was large rock masses and large stones buried in sand. Here the numbers of *Procerodes* were much lower. With the reappearance of a more suitable substratum in pool I, the numbers again increased, though the population was not so dense as in pools E and F. Finally, in pools J and K the large rock masses reappeared and *Procerodes* finally died out. Below these pools the shore was entirely rocky and no more *Procerodes* could be found.

Pantin (**15**) has pointed out that *Procerodes* is most abundant where the alternation between sea water and fresh water is most rapid. This is the case in the present instance also (e.g. the populations of pools E and F, where the alternation is very rapid—see below), but a more potent factor appears to be the nature of the substratum. This point has been emphasized above and it is supported by the fact that *Procerodes* can occur where no alternation of sea and fresh water is possible, but where the substratum is suitable (e.g. the brackish-water pool mentioned under (*b*) above).

As a supplement to these observations on the zonation of this estuarine form, readings were taken, at approximately half-hourly intervals for 12 hours, of the chloride concentrations of the rock pools. The detailed results are summarized in Table 15 and shown graphically in Fig. 4. Most of the observations were made in pool E, as here the alternations in the type of water were most marked and the population of *Procerodes* was at its highest. Supplementary readings were made for pools F and I. The distance from high-water mark spring tides to the water's edge is also plotted on the graph. The curve is flat-topped because during the period that the tide was out measurements

were made to the top of the highest permanent pool on the shore (pool E). A complete curve of tidal height would be approximately parabolic.

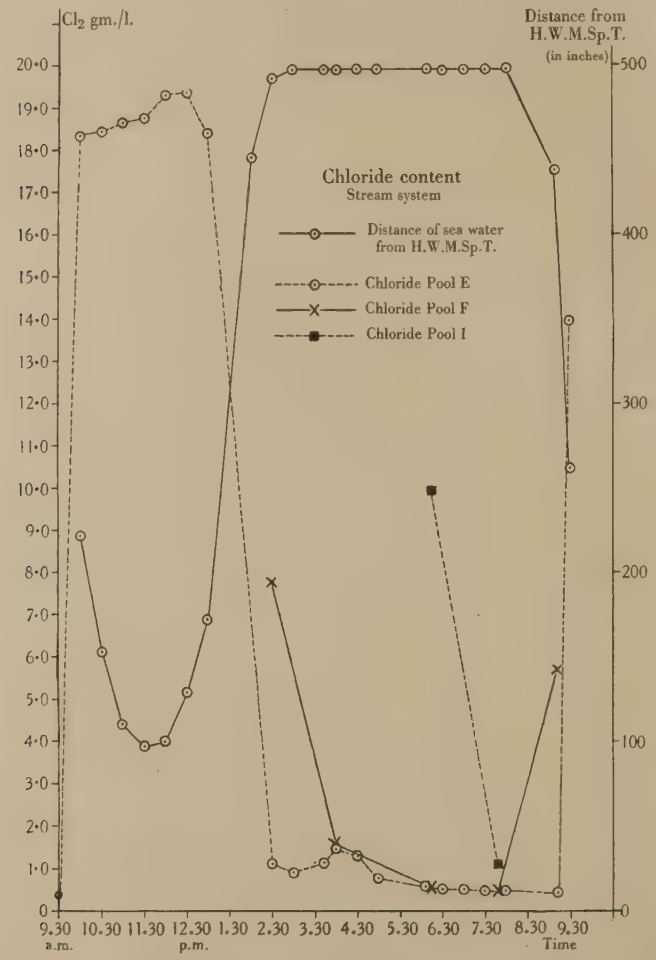

Fig. 4. Chloride concentrations of rock pools during a tidal period.

The curve for chloride in pool E shows how rapid is the environmental change that *Procerodes* has to withstand. In the morning, the concentration of chloride in the pool varied from 0·34 g. Cl_2/l. to 18·38 g. Cl_2/l. within half an hour, and again in the evening there was a change from 0·42 g. Cl_2/l. to 13·98 g. Cl_2/l. within a quarter of an hour. The change back again, from sea water to

Table 15. *Concentration of chloride in rock pools*

Readings taken between 9.30 a.m. and 9.30 p.m. on 19 July 1935.
All results expressed in g. Cl_2/l.

Pool	Time	Chloride	Distance of water from high-water springs (in in.)
E	9.30 a.m.	0·34	—
,,	10.0 ,,	18·38	222
,,	10.30 ,,	18·46	153
,,	11.0 ,,	18·66	110
,,	11.30 ,,	18·75	97
,,	12.0 noon	19·30	99
,,	12.30 p.m.	19·35	128
,,	1.0 ,,	18·38	172
,,	2.30 ,,	1·112	492
,,	3.0 ,,	0·919	497
,,	3.45 ,,	1·145	497
,,	4.0 ,,	1·452	497
,,	4.30 ,,	1·297	497
,,	4.55 ,,	0·768	497
,,	6.10 ,,	0·582	497
,,	6.30 ,,	0·500	497
,,	7.0 ,,	0·502	497
,,	7.30 ,,	0·465	497
,,	8.0 ,,	0·472	497
,,	9.15 ,,	0·423	437
,,	9.30 ,,	13·98	262
F	2.30 ,,	7·78	—
,,	4.0 ,,	1·542	—
,,	6.15 ,,	0·574	—
,,	7.50 ,,	0·458	—
,,	9.15 ,,	5·665	—
I	6.15 ,,	9·965	—
,,	7.50 ,,	1·111	—

fresh water, is almost as rapid. There is a minor rise in the chloride concentration between 3.30 and 5.0 p.m. approximately. It is just possible that this may be connected with the weather conditions at the time, as during this period a sudden squall of rain, accompanied by a strong south-west wind occurred. On this part of the coast such a wind would drive the waves closer inshore and so increase slightly the chloride concentration for a short period.

In pool E, *Procerodes* is exposed to sea water for approximately $3\frac{1}{2}$ hours and to water that was almost fresh (the chloride concentration of the water never quite fell to that of the water in pond 6, the concentrations were: 0·34 g. Cl_2 l. (pool E) and 0·13 g. Cl_2 l. (pond 6)) for approximately $8\frac{1}{2}$ hours during one tidal period.

The supplementary observations on the lower pools F and I show that there is a similar rapid change during the tidal period, but that the period of exposure to fresher water was, naturally, reduced to approximately $2\frac{1}{2}$ hours in pool F and to less than an hour in pool I. All these observations were made on 19 July, a date half-way between the spring tides and the neap tides, so that they represent average values for exposure. The periods of exposure to the two types of water would, of course, vary slightly at the spring or neap tides.

The damming of the stream feeding pond 6 to provide a drinking place for sheep and cattle, which occurred between July and September, had a profound

effect on the *Procerodes* population. In September, no stream was leaving pond 6, with the effect that pools A and B were practically dry, pools C and D had disappeared and pool E and the upper part of pool F were dry except at high tide. Under these conditions, the planarians retreated downwards when the tide was out and were to be found under smaller stones (1–2 in. in diameter) some little distance below the surface. As the tide rose, a migration to the surface took place, followed by a slow migration downwards as the tide fell and the surface stones dried. At this time too, it was found that a migration up the shore was taking place and that *Procerodes* could now be found in the lower 3 ft. of the "desert" area of shingle, again below the surface on the smaller stones.

Since in every case the individuals examined were active and healthy, it is apparent that *Procerodes* can withstand at least two completely different sets of conditions. A detailed examination over a longer period would undoubtedly show other migrations in connexion with local conditions. During further work on the island in April 1936, the series of ponds was again examined. After a winter of heavy rain, the stream was full and running rapidly over the shingle and down through the rock pools. *Procerodes* was again present under the larger surface stones, so that it seems that the whole system had returned to the state of the previous spring and summer.

Throughout the season the calcium content of pond 6 was high. Pantin(**15**) considered that a high concentration of calcium was necessary for *Procerodes*, but Ritchie (**13**) has since shown that this is not absolutely essential, as this planarian can occur in streams where the concentration of calcium is as low as 5·0 mg./l.

6. Acknowledgements

In conclusion, I wish to express my thanks to many people who have helped in this work: the Trustees of the Hon. F. G. Wynn for allowing the work to be carried out on the island; Mr F. Loxham Kidd for much help during the April visit; the Air Ministry for the meteorological data quoted in the paper; and the following for their assistance in the identification of material: Mr Charles Oldham (Lamellibranchiata), Prof. Aug. Thienemann (Chironomid larvae), Prof. W. M. Tattersall (*Asellus*), the late Mr H. Parry Jones and Mr W. E. China (Hemiptera) and Mr H. D. Slack (Trichoptera).

Finally, it would be ungrateful not to mention the very ready help given by many people, both on the island and on the adjoining mainland, without which both collecting and the transport of material and apparatus would have been impossible.

7. SUMMARY

1. An account is given of the chemical changes and the fauna of a series of small ponds on Bardsey Island (Caernarvonshire) during 1935.

2. It has not been possible completely to analyse the environment of each pond, but certain controlling factors have been outlined. The chief points stressed are:

(*a*) The great variation in the environment from one pond to another, as each is influenced to a considerable extent by purely local conditions.

(*b*) The rigour and rapidity of the changes taking place during the period reviewed.

(*c*) The effects of the drying of the ponds.

3. The fauna is rather restricted, but has several points of interest:

(*a*) The occurrence of *Gammarus chevreuxi* only, truly freshwater species of *Gammarus* being absent.

(*b*) The occurrence of *Asellus meridianus*, and the absence of *A. aquaticus*.

(*c*) The large numbers of Corixidae that occurred in the shallower, exposed ponds inland.

4. In addition to this general account. the factors controlling the distribution of the flatworm *Procerodes ulvae* are discussed.

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THE RELATIONS OF SOME NATIVE INSECTS TO INTRODUCED FOOD PLANTS

By HAROLD M. HEFLEY

(*University of Oklahoma, Department of Zoology*)

1. Introduction

Van Deventer (1933) was one of the first to call attention to the changes wrought by civilization on primeval communities. His investigations reveal that with the introduction of civilization into primitive areas, the large, slow-multiplying mammals are the first forms to go, and these are followed by much of the climax vegetation and the associated invertebrate forms. Man brings into an area a group of organisms which may be called ecologic "camp-followers", and these in turn modify the original communities, change the natural sequence of succession, and may in some instances eliminate the endemic vegetation entirely.

The present investigation reveals how certain insects native of North America have managed successfully to meet the changes produced in a primitive area by the invasion of two plant forms introduced into the Western Hemisphere by man. The area studied was a portion of the Canadian River floodplain approximately 15 miles long by 3 miles wide, between Cleveland and McClain Counties, Oklahoma, U.S.A. The centre of the area is 4 miles due west of the University of Oklahoma Campus.

The floodplain of the river is unique in many respects. Before the country was opened to settlement in 1889, the floodplain presented a very different picture to that at the present time. Extensive forests grew almost to the water's edge in many places, and on the higher levels were subclimax patches of blue-stem (*Andropogon furcatus*) prairie, the grass higher than a man's head. The river had water actively flowing during the entire year, and the bed ("sand-bar" in local parlance) was less than 150 yd. across. The floodplain originally had three definite levels: the bed of the river, an intermediate pseudo-terrace some 5–8 ft. above the bed, and a true terrace 8–12 ft. above the pseudo-terrace.

Civilization has changed this state of things to a remarkable degree. Ploughing and over-grazing of the uplands in the river basin caused a greatly increased run-off, which in turn produced devastating floods. The largest flood occurred in 1906 when torrential rains swelled the waters to a breadth of nearly 5 miles over the area. All of the timber on the pseudo-terrace was swept away (an area three-fourths of a mile to a mile wide and about 7 miles long), and much cutting on the river terrace took place also. As a result a desolate sand bar nearly 2 miles in width, with only drifts of uprooted trees remained.

The river then added another level to the three already present: a level intermediate in height between the bed and the pseudo-terrace. For the sake of convenience the bed has been designated as the first level, the one added after the 1906 flood as the second, the pseudo-terrace as the third, and the true terrace as the fourth level. The second level varies in height from a few inches to 4 ft. above the river bed; the third level is from 1 to 8 ft. higher than the river bed; while the fourth level is from 9 to 16 ft. higher than the river bed level at the present time. The second level is formed from the first by the deposition of wind-blown sand on the wet low bar of the stream, and the third is formed by this means with the addition of plant remains. It is really a more advanced (older) portion of the floodplain and built to a higher level by physiographic and biotic agencies. The fourth level varies greatly in age; portions of it are probably of late Pleistocene age, while other parts of it are much younger.

Since 1906 the floodplain has been invaded by two plants introduced by man. These are the tamarisk (*Tamarix gallica* L.) and the sweet clover (*Melilotus alba* Desr.). The former is a native of the Eastern Hemisphere, and related species (*Tamarix pallasii* and *T. hohenacherii*) occupy positions on the Kura river (Karabakh Steppe) similar to those now occupied by *T. gallica* on the Canadian River floodplain. Tamarisk was from all accounts introduced into the south-western United States by the early Spanish settlers. It has now escaped from cultivation, and appears to be well on the way to changing the succession of the floodplain sere by forming initial communities on the second and third levels. Since the plant is quite intolerant, it produces thick tangled thickets, and eliminates the natural vegetation by competition and shading.

Sweet clover forms extensive facies on the mid-seral communities on the third level, and to some extent chokes out the native vegetation. Since it is a biennial, however, it must needs be confined to mid-seral associes, and cannot compete with perennial climax and subclimax vegetation. The plant is of European origin and was introduced into the United States by the early colonists. It is extensively used as a pasture plant, is cut for hay, and is planted in many places for honey. In Oklahoma it has escaped from cultivation and grows along roadside ditches, in waste fields, and especially on the third level of the Canadian River floodplain. The plant is quite hardy, and re-seeds itself year after year.

2. Methods

Two methods were employed in collecting the data presented here. In the case of the smaller insects that do not fly when disturbed, the sweep-net method of collecting was used; 50 sweeps with a net 40 cm. in diameter and a handle 1 m. long was taken as a standard, or unit collection. The method of sight counting was used to determine the number of wary insects, in this case, locusts. An area was carefully approached, the number of locusts counted and

recorded. The area was afterwards measured. In addition to these methods numerous cruisings were made on foot over the entire area; observations were taken and recorded.

Collections were made in a third-level tamarisk consocies, and others were taken in contiguous communities composed of native vegetation (150 yd. distant from the tamarisk community) on the same days. The data are compared in Table 1. Collections were made in a sweet-clover facies of a third-level *Salix-Populus-Andropogon-Panicum* Associes, *Andropogon-Panicum* Associes, and *Salix-Populus* Associes and control collections were taken in a different portion of the communities (50 yd. distant) that contained no sweet clover. These data are presented in Table 2.

3. *Tamarix gallica*

The insects discussed below were present in the tamarisk consocies in numbers sufficient to be of importance in imparting a physiognomy to the community. A total of 45 native insects were associated with tamarisk, the majority of them in small numbers.

Chlorotettix viridis Van Duzee.

This leafhopper was the most abundant form associated with tamarisk. It is usually associated with sedges and grasses in low, moist places. Collections made on the same days showed that there were from 50 to 3000 times more leafhoppers in the tamarisk than in the native vegetation. They were present in such numbers that during the summer of 1934 complete defoliation was effected over large areas of the consocies. There is no doubt that *C. viridis* has a decided preference for the introduced plant over the native vegetation on which it formerly fed.

Ceratomegilla fuscilabris Mots.

Ladybirds of this species fed extensively on the nymphs of the leafhoppers. Their presence in the tamarisk consocies was caused by a plentiful supply of food. They occurred in numbers from 1 to 38 times larger than in the contiguous associes of native vegetation.

Thyridopteryx ephemeraeformis Haworth.

"Bagworms" are very promiscuous feeders, evidencing an especial fondness for the conifers (Holland, 1904). In central Oklahoma they feed on elm, willow, cotton-wood, juniper, and a variety of other plants. They prefer willows (*Salix longifolia* and *S. nigra*) to the rest of the endemic vegetation on the floodplain. Counts made on square metre quadrats in tamarisk and willow thickets of comparable height and density revealed from 1 to 199 bags per sq. m. in willows, and from 0 to 674 bags in tamarisk during the yearly cycle (Table 1).

Table 1

Figures for *Thyridopteryx* are bags per sq. m. containing live larvae, pupae, females, or ova. All the others are numbers taken in 50 sweeps

	1933						1934								
	Oct. 19	Oct. 28	Nov. 6	Nov. 15	Nov. 28	Dec. 12	Feb. 4	Mar. 11	Apr. 21	May 21	June 18	July 19	Aug. 26	Sept. 15	Oct. 4
Tamarix consocies															
Chlorotettix viridis	51	30	33	28	21	45	—	—	—	53	1051	4259	375	308	275
Ceratomegilla fuscilabris	—	—	—	—		—	—	1	1	3	38	17	2	1	—
Thyridopteryx ephemeraeformis	—	—	4	4	1	—	—	36	674	326	300	170	96	29	27
Pachybrachys hepaticus	—	—	—	—	—	—	—	—	15	6	4	6	—	—	—
Paria sexnotata	1	—	—	—	—	—	—	2	1	1	4	—	—	1	—
Oecanthus 4-maculatus	—	5	1	2	—	—	—	—	—	—	5	3	—	1	1
Lygus pratensis	—	—	—	—	—	—	—	—	—	15	13	—		—	—
Control associes															
Chlorotettix viridis	6	4	1	7	—	9	—	—	—	160	110	150	35	111	230
Ceratomegilla fuscilabris								None							
Thyridopteryx ephemeraeformis	—	—	3	3	2	2	1	1	199	189	162	90	79	32	20
Pachybrachys hepaticus	—	—	—	—	—	—	—	—	10	5	—	1	6	2	—
Paria sexnotata	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Oecanthus 4-maculatus								None							
Lygus pratensis								None							

Table 2

Figures for *Empoasca* are numbers taken in 50 sweeps. All the rest are counts per sq. m.

	1933								1934									
	Oct. 3	Oct. 17	Oct. 24	Oct. 31	Nov. 7	Nov. 21	Dec. 4	Dec. 14	Feb. 17	Mar. 9	Mar. 20	Apr. 9	Apr. 29	May 30	June 29	July 4	Aug. 4	Sept. 8	Oct. 6
Melilotus alba (Facies in *Andropogon-Panicum*; *Salix-Populus*; and *Salix-Populus-Andropogon-Panicum* Associes)																			
Stictocephala lutea	2	7	2	—	13	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Schistocerca americana	1	—	—	—	1	—	—	1	—	1	—	—	—	7	12	9	11	2	1
Schistocerca obscura	—	—	1	—	—	—	—	—	—	1	—	—	—	3	7	10	4	1	1
Melanoplus differentialis	7	2	1	—	1	—	—	—	—	1	—	3	2	6	13	3	7	5	—
Melanoplus bivittatus	—	2	—	1	—	—	—	—	—	—	—	—	—	1	5	6	6	—	—
Empoasca maligna	—	—	—	—	—	—	—	—	5	6	—	50	71	14	—	3	—	—	—
Control associes																			
Stictocephala lutea										None									
Schistocerca americana	—	—	—	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Schistocerca obscura	—		1		—	—		—	—			—	—		2	—	1		—
Melanoplus differentialis	3	—	3	—	—	—	—	—	—	—	—	—	—	6	—	6	—	—	1
Melanoplus bivittatus	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Empoasca maligna										None									

Pachybrachys hepaticus Melsh. and *Paria sexnotata* Say.

These beetles were present on the flowers of the tamarisk from May until September. They were observed feeding on the pollen of full-blown flowers as well as on unopened buds. Their native food plants are not definitely known, but both forms are usually found in prairie vegetation.

Oecanthus quadripunctatus Beautenmuller.

Blatchley (1920) records Oecanthids as feeding on Aphids. The writer observed them devouring the pollen of tamarisk and also drinking honeydew produced by leafhopper nymphs (*Chlorotettix viridis*). They were not taken in the control community of native vegetation.

Lygus pratensis Linn.

Lygids were taken from tamarisk flowers during the months of May and June. They are normally present in grassland communities. The bugs were observed to suck either sap or nectar from the tamarisk blooms. Since their food plants are not limited (they feed on a large variety of native grasses) little can be said save that they exhibited a decided preference for tamarisk flowers during the summer months, and were absent from contiguous communities of mixed grass and willow during the summer period.

4. *Melilotus alba*

The insects which were associated with sweet clover were not as marked in their preference of the introduced plant over the native vegetation as were those associated with tamarisk. A total of 39 species of insects were taken in facies of sweet clover in floodplain communities. Of these, only 6 occurred in sufficient numbers to impart much of an aspect or physiognomy to the sweet clover facies.

Stictocephala lutea Walker.

These large Membracids were commonly found during the nymphal and imaginal stages feeding on green briars (*Smilax rotundifolia* Linn. and *S. glauca* Walt.) and mulberry (*Morus rubra* Linn.). They were present in rather large numbers during the late summer and fall, in patches of sweet clover, and were observed feeding on the tender young stems. The insects were also found to hibernate in the duff beneath the sweet clover during the winter.

Schistocerca americana (Drury) and *S. obscura* Drury.

These two large locusts normally inhabit grassland. *S. americana* is more often associated with species of *Andropogon*, while *S. obscura* is more partial to willow, cotton-wood, and groundsel tree (*Baccaris halmifolia* Linn.). During the period from June until mid-August the nymphs of both species were common in facies of sweet clover and actively engaged in devouring it. The adults were likewise seen feeding on the plants in the fall and early winter.

Melanoplus differentialis (Thomas) and *M. bivittatus* (Say).

Like most grasshoppers, these two species of *Melanoplus* were by no means restricted to any particular food plant, but preferred lush, rank, bottom-land vegetation. It was not surprising, therefore, to find both adult and nymphal Melanoplids among the sweet clover in the floodplain communities. In several locations, these, together with the Schistocercids, completely stripped the clover of leaves, and devoured the more tender parts of the stems.

Melanoplids as well as Schistocercids occurred in communities composed of native vegetation during the times they were taken from sweet clover, but in somewhat smaller numbers (Table 2).

Empoasca maligna Walsh.

This Cicadellid was commonly found associated with wild and cultivated grape vines (*Vitis* spp.) and also to some extent among upland prairie vegetation. During April and May it was swept in large numbers from sweet clover growing in the floodplain communities. It was not found in near-by associes, and was taken only in one other situation on the floodplain; in a clump of willows on which wild grape vines were growing.

5. Discussion

The 13 species of insects discussed above are those which occurred in the greatest numbers on two introduced plants in the Canadian River floodplain. Many other species were taken from both tamarisk and sweet clover, but these were present in such small numbers that it is impossible to say whether they were present by design, or accident.

The behaviour of the forms which utilize the introduced plants as a source of food, however, raises some rather interesting speculations. With the elimination, or reduction of the numbers of plants on which an insect normally feeds, and to which it is probably exclusively attached, one would expect a corresponding reduction in the numbers of the insect. This sort of behaviour does occur in species that are restricted as to their food plants. Other insects, while having their preferences, will devour something less palatable if the preferred food is not available.

When insects native to an area quit the endemic vegetation in favour of introduced vegetation, the question which presents itself is, what caused them to do it, when the food material they are accustomed to is present in plenty? There are apparently two possible answers. One is that the behaviour of the insect forms is the result of active food selection on their part; that they found something new, tasted it, and found it good. The other explanation is that during the time that has elapsed since a species of insect evolved into its present state, and preyed upon one plant (or at most a few), a natural resistance has been evolved by the plant toward the forms which prey upon it. This supposition would suit admirably in the case of Heteroptera and

Homoptera that inject salivary juices into the plants when feeding, but the writer fails to see how a plant could become resistant to leaf-eating beetles.

It is interesting to note that the insects which manifested the greatest affinity for the introduced plants *are* Homoptera, and Coleoptera and Orthoptera (chewing insects) *did not show* such marked affinities. The data seem to indicate that both factors are probably responsible for certain insects favouring the tamarisk and sweet clover more than the endemic vegetation. Until much more work has been done, however, the writer feels that conclusions less general than these would be premature, and based on insufficient data.

6. Summary

1. A study of the biota of the Canadian River floodplain in Oklahoma showed that two introduced species, tamarisk (*Tamarix gallica*) and sweet clover (*Melilotus alba*), are important factors in community succession in that area.

2. Associated in large numbers with these introduced plants are 13 species of native insects which apparently show a preference for these introduced plants rather than for their original food.

3. Homoptera showed the greatest affinity for the introduced plants, while chewing insects (i.e. Coleoptera and Orthoptera) did not show such marked preferences.

4. The reasons for the preference for the new plants are not clear.

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THE PRESENT STATE OF THE NEWFOUNDLAND SEAL FISHERY

By J. S. COLMAN

(*With* 8 *Figures in the Text*)

1. Introduction

The Newfoundland seal fishery, while of considerable antiquity, is neither the oldest nor the most important industry of the country. Nevertheless, it brings some two or three hundred thousand dollars into the country just when they will do most good, at the end of the winter when the fishermen are preparing to fit themselves out for the summer's cod fishery.

The seal fishery used to be much larger and more important financially than it is now, as will be shown later, and there is considerable conflict of opinion as to whether it has been suffering a merely temporary decline or is in serious danger of dying out. After a bad season, one captain may utter grave warnings that the seals are being exterminated, while another will maintain that the seals are as numerous as ever, but have been hard to come by.

In view of these differences among experts, it seemed worth while to examine the records of the sealing fleet as far back as possible, to see if this would give any indication of long-period changes in the success of the fishery.

Fortunately, the records of the steam sealing fleet are remarkably complete back to the first use of steam sealers in 1863. Their compilation has been the patient labour of Mr Levi Chafe of St John's; they are published in his *Sealing Book* (of which a copy is available in the Bureau of Animal Population at Oxford) and are added to year by year. This book is a mine of information about the sealing industry and has formed the principal basis for the present paper. For information concerning the habits of the seals off Newfoundland I am indebted partly to Mr W. A. Munn's introduction to the second (1923) edition of the *Sealing Book*, but chiefly to Nansen's *Hunting and Adventure in the Arctic* (1925).

The present paper is no more than a review of known facts, and is an attempt to clarify the prevailing uncertainty as to the state of the fishery. In any one year, as will be shown below, the success of the fishery depends on several factors, such as the type of ship used, the thickness of the ice, the weather conditions and, above all, on the number of men fishing. In the long run, the answer seems to be that at the present time and at the present rate of fishing the seals are a little more than holding their own.

2. History of the seal fishery

The Newfoundland seal hunt has for a long time been an annual event in the lives of the people, and occupies a month or 6 weeks in March and April. Very few seals were caught in Newfoundland before the eighteenth century, because there were very few settlers, and the crews who used the place as a summer fishing station did not arrive until after the seals had returned north.

By about 1750, however, quite a number of seals were being caught in nets from the shore during their annual migration southwards to the Grand Banks. Towards the end of the century the first great advance in the fishery was made when schooners began to be used for getting out to the ice on which the seals bring forth their young. This not only brought the sealers to where the seals were most abundant, but also enabled them to capture the newly born young, or "whitecoats", whose fur is far more valuable than that of the adults. The principal source of wealth from the seals, however, is their oil.

The schooners became more numerous and larger, up to 150 or 200 tons in some cases, and by 1830 many of the villages and towns of Conception Bay, particularly Brigus and Harbour Grace, and other places on the east coast, were sending vessels to the fishery. St John's was not backward, but had not then attained the pre-eminent and monopolistic position it holds to-day.

The second quarter of the nineteenth century was the heyday of the seal fishery. Upwards of 300 schooners were sailing from St John's and Conception Bay, with 12,000 men or so in the crews, and they were regularly bringing back over half a million seals.

In 1863 the second advance in the methods of the seal fishery occurred, when steamers were used for the first time. These were small, wooden ships, Dundee built, of 200–300 tons, but more and larger ones were built and they soon showed their superiority over the schooners. If a schooner got a full load of seals, she made more profit per man than a steamer owing to her very low running cost; but should she find the ice conditions bad and be unable to find the seals, she might easily catch nothing at all, and stood a good chance of being crushed in the ice.

The steamers, on the other hand, were strong enough to withstand all but the heaviest ice pressure, and could also force their way through ice in order to find the seals. Although they were never likely to make the extravagant profits possible to the schooners, they were much less likely to come home "clean", and in the long run steam was found to be a better investment than sail.

By the beginning of the present century, the old wooden steamers were finding it increasingly hard to keep down repair bills for ice damage, and year by year one or other of them at last got crushed too badly and had to be abandoned. This encouraged the third great step forward, which was the use of steel ships. The wooden ships were accustomed to break up the ice by main force, by ramming, but the new steel vessels had the fore-foot cut away so that

they could ride up over the ice and crush it by their weight, a much less arduous way of making a channel, but also requiring a great increase in power and a corresponding increase in running costs. However, as compensation for this, the wooden steamers can follow up through the channels cut by the steel ships, and so reach seals which they would otherwise be unable to obtain. Last year's fleet (1936) consisted of three steel vessels and five veterans of the old wooden fleet, including the world-famous "Terra Nova" of Antarctic renown.

3. The seals

Two species of seal are hunted off Newfoundland, the Harp, Saddleback, or Greenland seal, *Phoca groenlandica*, and the Hood or Bladder Nose, *Cystophora cristata*. These are always known as harps and hoods respectively in Newfoundland. Their distribution and habits are very well and fully described by Nansen in his *Hunting and Adventure in the Arctic*. Young harps usually make up about nine-tenths of the total catch.

Both are migrating seals, and in both the young, before they enter the water, are more valuable than the adults. For one thing their skins render clearer and, weight for weight, more abundant oil, and also at this stage the young harps are covered with a thick white wool which is valuable as fur, whereas the adults have only coarse hair in much less demand. These young harps are known as "whitecoats" and are the principal object of the fishery.

In the case of the harps, the whitecoats are quite helpless for the first three or four weeks and need the constant care of their mothers, until they shed their wool and grow coarse hair instead. Then they enter the water, learn to swim and soon start catching fish for themselves. The young hoods are not quite so helpless in their early days, but they do not wander far until they are fully a month old. For the next several years the seals are growing up, and do not start breeding until they are at least four years old. During this time they have not got the distinctive markings of the adults, and both species are then known as "bedlamers". This curious word is apparently a corruption of *bêtes de la mer*, the name given to them by the Channel Islanders, Bretons and Basques, who were fishing these waters long before the English came. The bedlamers follow in general the migrations of the breeding seals, but in a rather less organized way.

The harps are distributed over most of the colder parts of the North Atlantic, and have three well-defined breeding grounds: the most easterly is in the mouth of the White Sea, where the young are brought forth from the middle of February on; the central one is to the north of Jan Mayen Island, and here the pups appear about 3 weeks to a month later than in the White Sea; the western grounds, by far the most prolific, are to the north-east of Newfoundland, off the Funk Islands, and also to a lesser extent in the Gulf of St Lawrence.

The first sign of the harps is their appearance off the coast of Labrador

in the latter half of November, moving south. At this time of year there is no ice to impede them, they are helped by the Labrador Current and their progress is extremely rapid. The whole procession of possibly some millions of seals will sometimes pass any one place within a week.

At the Straits of Belle Isle, between Newfoundland and Labrador, some of the seals turn westwards into the Gulf of St Lawrence, but the majority proceed southwards along the coast and islands to about the mouth of Trinity Bay. Then they work out to sea and find their way to the Grand Banks, where they arrive about the New Year. Later on they are joined by some of the seals which have come round by the Gulf of St Lawrence and Cabot Straits, and they all stay on the Banks for a month or more, eating voraciously and building themselves up for the whelping and mating season, during which they eat very little for several weeks.

Then, during February, they work north until they reach the ice off the Funk Islands, and the females give birth to their young on this ice from about the beginning of March. This is about a week earlier than the seals in the Jan Mayen area, and about a fortnight later than those in the White Sea. As these dates remain constant within a few days in each of the grounds from year to year, it appears that there must be three separate tribes of seals, each with its own breeding grounds, and not intermingling to any great extent.

The hoods or bladder noses are less important to Newfoundland than the harps, being both less numerous and more difficult to secure. They pursue somewhat similar migrations to those of the harps, but keep further off shore. Their breeding time is 2 or 3 weeks later, and the grounds are more scattered and again further away from the land. The young hoods do not possess the valuable coat of white wool, but are hairy from birth and can swim within a day or so. The distribution of the hood seals is also confined to the colder parts of the North Atlantic, but is less extensive than that of the harps, for hoods are not found near Spitsbergen or off Northern Russia. The known breeding grounds of this seal do not seem sufficient to account for the enormous numbers found at other times, such as June and July, in the Denmark Straits between Iceland and Greenland, when they are moulting; Nansen believed that there may be a very extensive breeding ground somewhere in Davis Straits which has not yet been either discovered or exploited. At the end of the present paper it is suggested that there may be a similar reserve of harp seals.

The males of both harps and hoods accompany the females to the breeding grounds; they protect the females to a certain extent, and as soon as the young have been weaned mating takes place, pregnancy lasting a little over 11 months.

4. Methods of hunting

The principal object of the fishery is the young seals, and these are hunted while on the ice. The ship is worked as close to the seals as possible, and the men then go among the whitecoats and hit them over the head with clubs

called "sealing bats". The skins are collected together in heaps or "pans" on the ice, marked by flags bearing the ship's name, and the men then go off after more seals. In this way they may go so far from the ship that they have to spend a night on the ice; should a blizzard spring up or fog come down there will be very considerable danger, and in the past there have been a number of disasters when parties of men have got lost and have died of exposure.

Since the whitecoats make no effort to get away, they can be completely wiped out in any one patch of breeding seals. Sometimes a hundred thousand may be killed in the course of a day or two, and then several days must elapse before the skins can all be collected, brought on board and stowed down. When possible, the ship will work her way through the ice from pan to pan, but sometimes, if she is fast in the ice, the pelts have to be brought to the ship. This means several journeys by the men, hauling heavy loads of seals for miles over rough ice. All in all, the Newfoundland seal fishery is as hard, dangerous and uncomfortable a trade as is pursued anywhere. Nevertheless there are usually far more men applying for berths than there are berths for them.

When the whitecoats lose their wool and take to the water, the sealers concentrate on the older seals (though to a lesser extent than was formerly the case), hunting them with guns and by stealth. In this way many are captured, but many more, though killed, sink into the sea and become a dead loss both to the seal herds and to the fishery. Many of the pans of skins on the ice are often lost, too, if the ice breaks up and spills them into the water.

It will be seen that the seal fishery is about as destructive in its methods as possible. The new-born young are the principal object of the hunt, and no protection is afforded to female seals or to seals which are not old enough to have bred. In addition, of the seals killed, a considerable proportion, sometimes as many as a third of the whole, is lost irretrievably. Since the seals are slow breeders, it might be expected that a century of such methods would have caused a dangerous diminution in the numbers of the seal herds. This will be discussed below.

5. THE SCHOONER SEAL FISHERY

The schooner sealing fleet did not amount to very much until the early years of the nineteenth century. Up till then only boats and open sailing vessels had been used, and the success of the seal hunt depended on the wind blowing the "whelping ice" close inshore. When decked schooners came into use, however, they could go further afield and stay out longer, and the men were no longer so dependent on the seals coming within reach. By the 'thirties, schooners of 100 tons were being built, and during the next 30 years there were in use brigantines, brigs and even barquentines of between 200 and 300 tons.

At that time more of the seals were shot than at present. As has been pointed out, this practice was not only destructive but also wasteful in the highest degree. As a rule, only about a quarter of the seals killed by the

gunners were recovered, and since many of these were bedlamers, which had not yet had a chance to breed, this practice was probably one of the main reasons for the diminution in the seal population by the 'sixties. This depopulation is shown in Table 1, which gives the number of seals caught in several years between 1815 and 1862. The largest seal catches were during the 'thirties and 'forties, but the largest fleets were not sailing until the 'fifties: in 1857 there were 400 vessels with 13,000 men engaged.

Table 1. *Numbers of seals taken by schooners in several years between* 1815 *and* 1862, *inclusive*

Year	Seals taken	Year	Seals taken
1815	126,315	1844	585,530
1820	213,679	1848	521.004
1822	306,982	1852	534,378
1826	222,007	1855	298,083
1829	357,523	1856	361,317
1830	558,942	1858	507,624
1831	686,836	1859	329,185
1832	508,407	1860	444,202
1836	384,321	1861	375,282
1840	631,375	1862	268,624

By the 'sixties, the seals were no longer so easy to come at, and their numbers may have been seriously diminished. It is idle to blame the decline of the seal fishery, as not a few sentimentalists have done, on the use of steam in place of sail. So long as the seals were numerous enough to be picked up easily by the schooners, there was no call for the more expensive steamers. Not until it became necessary to force a way through the ice to find more distant seals did steamers become an economic proposition.

By the 'eighties, the schooner fishery was virtually extinct.

6. The steam fishery

The use of steamers commenced in 1863, with 2 ships. These were gradually added to, until by 1871 the steamer fleet was established; in that year 15 vessels, with a total tonnage of 3826 and crews numbering 2051, brought back 253,707 seals (Table 2, and Figs. 1, 2, 3). From 1872 until 1914 there were never less than 18 steamers and 3000 men, and the number of seals caught varied between 126,628 in 1897 and 353,276 in 1900.

As will be seen from Table 2 and Fig. 3, the number of seals brought in varied widely from year to year, owing to a number of factors controlling the success of the fishery. First of all the seals do not occur in the same place from year to year, since the position of the whelping ice depends on currents and winds; winds round Newfoundland are extremely variable, and the volume of the Labrador Current also changes from year to year in a manner at present unpredictable. Then again, in a hard winter, the ice is apt to be thicker and more difficult to force a way through; last year (1936), which had a mild winter, presented ice which was loose enough, but there was an unusual amount of fog.

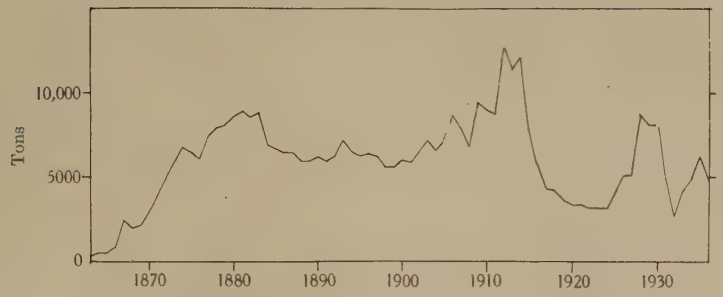

Fig. 1. Total tonnage of steam sealing fleet, 1863–1936.

Fig. 2. Number of men sealing, 1863–1936.

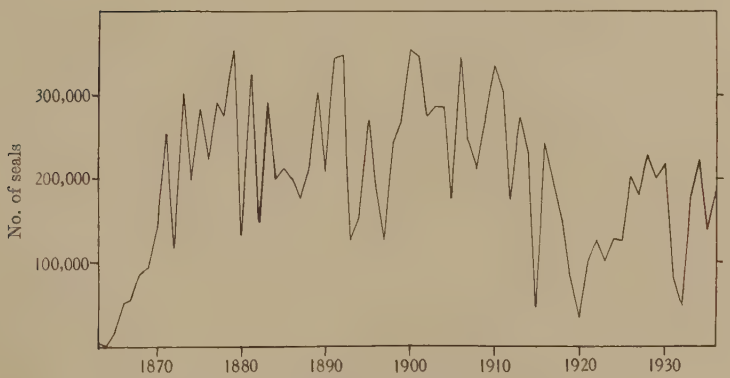

Fig. 3. Number of seal skins brought in, 1863–1936.

Yet another unpredictable figure is that of the pelts lost on the ice after being collected in "pans". In 1935 this loss was estimated at about 40,000.

Table 2. *The Steam Seal Fishery, including those vessels sailing out of Harbour Grace between the years* 1866 *and* 1895

Year	No. of vessels	Total tonnage	No. of men	No. of seals	Seals per man	Tonnage per man	Total value $	Share per man $
1863	2	363	210	4,340	21	1·7	—	—
1864	3	539	311	1,059	3·4	1·7	—	—
1865	3	539	323	19,086	59	1·7	—	—
1866	5	948	565	51,458	91	1·5	—	—
1867	10	2,422	1,255	56,550	45	1·9	—	—
1868	9	1,957	1,063	89,000	84	1·8	—	—
1869	10	2,107	1,163	95,270	82	1·7	—	—
1870	12	2,913	1,500	145,010	99	2·0	—	—
1871	15	3,836	2,051	253,707	124	2·0	—	—
1872	19	4,956	2,813	118,696	42	1·8	—	—
1873	21	5,986	3,683	301,442	82	1·7	—	—
1874	22	6,778	3,999	200,822	50	1·7	—	—
1875	22	6,482	3,880	282,990	73	1·8	—	—
1876	20	6,189	3,678	224,521	61	1·7	—	—
1877	23	7,426	4,656	291,246	63	1·6	—	—
1878	25	7,939	5,131	273,852	53	1·6	—	—
1879	25	8,037	5,162	353,229	68	1·6	—	—
1880	27	8,538	5,620	133,680	24	1·5	—	—
1881	27	8,852	5,815	325,979	56	1·6	—	—
1882	26	8,541	5,704	148,514	26	1·5	—	—
1883	25	8,308	5,683	291,768	51	1·5	—	—
1884	22	6,897	5,001	199,084	40	1·4	—	—
1885	20	6,646	4,620	213,433	46	1·5	—	—
1886	20	6,471	4,409	199,815	45	1·5	—	—
1887	20	6,471	4,211	177,084	42	1·6	—	—
1888	19	5,949	4,004	213,269	53	1·5	—	—
1889	19	5,949	3,848	303,046	79	1·6	—	—
1890	20	6,149	4,280	207,086	48	1·5	—	—
1891	19	5,949	4,221	344,073	82	1·4	—	—
1892	20	6,266	4,708	348,824	74	1·3	—	—
1893	22	7,116	4,962	128,339	26	1·5	—	—
1894	21	6,498	4,737	152,821	32	1·4	—	—
1895	20	6,147	4,362	270,058	62	1·5	—	—
1896	21	6,352	4,506	187,517	42	1·4	276,814	20
1897	20	6,232	4,672	126,628	27	1·3	162,822	12
1898	18	5,588	3,810	241,708	63	1·5	335,575	29
1899	18	5,588	3,503	268,881	77	1·6	342,378	33
1900	19	6,053	3,760	353,276	94	1·6	483,602	43
1901	19	5,898	3,836	345,055	90	1·5	388,895	34
1902	20	6,468	3,978	274,219	69	1·6	402,623	34
1903	22	7,199	3,378	286,230	85	2·1	449,797	44
1904	21	6,655	3,328	284,473	86	2·0	403,794	40
1905	22	7,165	3,532	177,100	50	2·0	311,224	29
1906	25	8,634	4,061	341,836	84	2·1	607,505	50
1907	22	7,968	3,685	245,051	67	2·2	455,210	41
1908	18	6,814	3,141	213,868	68	2·2	375,443	40
1909	20	9,464	3,580	269,302	75	2·6	458,020	43
1910	19	8,994	3,364	333,349	99	2·7	628,009	62
1911	18	8,727	3,973	304,591	77	2·2	494,075	41
1912	23	12,670	4,179	175,130	42	3·0	329,265	42
1913	19	11,472	3,609	272,965	76	3·2	493,846	46
1914	20	12,067	3,959	233,719	59	3·0	497,979	42
1915	13	7,878	2,932	47,004	16	2·7	93,479	11
1916	11	5,916	2,028	241,302	119	2·9	642,464	106
1917	12	4,390	2,131	196,228	92	2·1	516,717	81
1918	12	4,250	2,056	151,434	74	2·1	863,553	140
1919	10	3,599	1,719	81,293	47	2·1	278,145	54
1920	9	3,354	1,583	33,985	21	2·1	159,950	34

Table 2 (*cont.*)

Year	No. of vessels	Total tonnage	No. of men	No. of seals	Seals per man	Tonnage per man	Total value $	Share per man $
1921	9	3,440	1,264	101,452	80	2·7	171,243	45
1922	8	3,150	1,196	126,031	105	2·6	197,838	55
1923	8	3,150	1,224	101,770	83	2·6	209,136	57
1924	8	3,150	1,227	129,561	106	2·6	241,127	66
1925	10	3,899	1,505	127,882	85	2·6	269,467	60
1926	12	5,033	1,648	211,531	128	3·1	395,511	80
1927	9	5,125	1,634	180,459	110	3·1	297,423	61
1928	11	8,637	2,190	227,022	104	3·9	394,164	60
1929	12	7,152	2,154	201,856	94	3·3	359,920	56
1930	11	7,047	2,129	218,644	103	3·3	405,810	64
1931	8	4,863	1,268	83,077	66	3·8	121,115	32
1932	4	2,651	731	48,613	66	3·6	58,367	27
1933	6	4,119	1,122	176,046	157	3·7	191,912	57
1934	8	4,863	1,459	223,700	153	3·3	324,792	74
1935	9	6,225	1,784	140,751	79	3·5	169,816	32
1936	8	4,863	1,460	183,689	126	3·3	224,495	51

The steamer fishery reached its full development by about 1874, and for about 40 years remained at nearly the same level (see Table 2, and Figs. 1, 2, 3). The greatest numbers of seals the steamers ever brought in were 353,276 in 1900 and 353,229 in 1879 (in 1831 the schooners landed 686,836 skins); the largest number of men in the crews was 5815 in 1881, and the greatest total tonnage was 12,670 in 1912. By 1919 the tonnage had dropped to 3599. At the beginning of the War the Newfoundland sealing fleet had reached its peak, so far, of development. There were 9 steel vessels prosecuting the fishery, and some 10–12 wooden ships; but during the War this fine fleet became scattered on War service. Some were sold, some were torpedoed and some were lost through stress of weather. Since the War there has not apparently been enough money to be got from seals to warrant the construction of new vessels.

A problem not yet successfully solved is what to do with the sealing ships during the rest of the year. A large vessel is too expensive to make a good sealer, and a successful sealer is too small to use in general overseas trade, so that at present the sealing fleet is laid up completely idle for 10 months of the year. During January and February they are dry-docked one by one, then they pursue the seals, after which they repose in St John's harbour for the rest of the year.

One result of the small size of the sealing fleets since the War has perhaps been the salvation of the seal herds, as will be indicated below. Although the other factors controlling the number of seals caught are highly variable and sometimes decisive, in the long run the number of men hunting the seals is the most important, and there is a general correspondence between the number of men and the number of seals brought in (see Table 2, and Figs. 2, 3). Since the War the number of men has been fewer than at any time since 1872. In the 44 years from 1871 to 1914, inclusive, the number of seals brought in failed to exceed 200,000 on only twelve occasions. In the 22 years from 1915 to 1936, inclusive, the catch has exceeded 200,000 only six times.

If the number of seals caught per man (Table 2, and Fig. 4) is examined, the results are striking. From 1863 to 1914 more than 100 seals were caught per man on one occasion only—124 in 1871. From 1915 to 1936 this has happened on 10 occasions, with figures of 157 and 153 in 1933 and 1934 respectively. Fig. 4 shows a gradual increase in the number of seals caught per man ever since the War, following on a previous step up at the end of the last

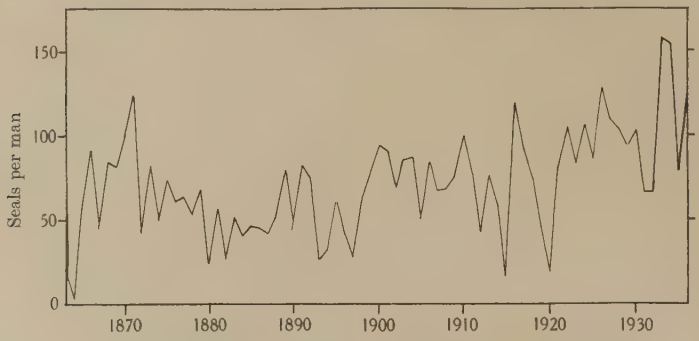

Fig. 4. Number of seal skins per man sealing, 1863–1936.

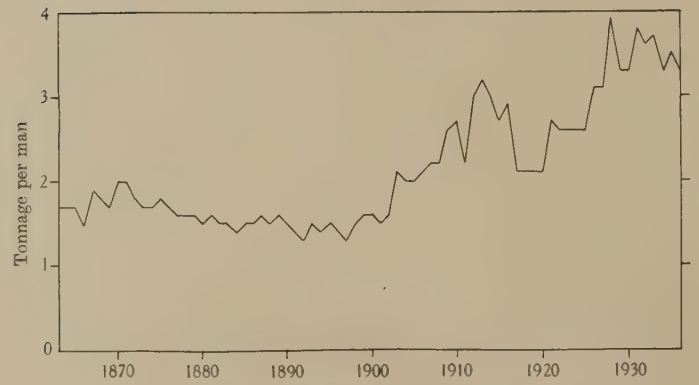

Fig. 5. Tonnage per man, 1863–1936.

century. The gradual increase of recent years has been due, I think, to the partial recovery of the seal herds on being not so intensively hunted, but the increase which appears about the year 1900 was partly the indirect result of legislation.

Until the 'nineties there were no regulations to control the number of berths for sealers, and the captains might take as many as they could squeeze in, the men sleeping in the hold, on the 'tween decks or anywhere else they could find under cover, and a small vessel of 200 tons would have a crew of 150 on board

for 6 weeks. When the seal pelts began to come aboard, the crew had to make way until by the end of a successful voyage the men would be sleeping all over the deck, in the boats, or even on the skins piled on the deck, in the most savage weather conditions. By 1900 the number of men was regulated, and since then the average tonnage per man has steadily increased, which must mean less inhuman accommodation than was formerly their lot (see Fig. 5).

Fig. 6. Net value of seal fishery, 1896–1936.

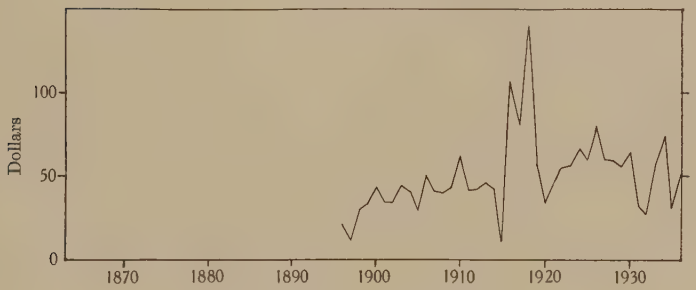

Fig. 7. Average share per man, 1896–1936.

An interesting result of this change has been the increased catch per man, and apparently there has been little or no effect from these regulations on the total number of seals caught. The increased catch per man has resulted in an increased share of the profits. Chafe's "Sealing Book" gives the value of the industry only from 1896 (Table 2, and Figs. 6, 7). In general it follows fairly closely the total number of seals caught (Fig. 3), since the price of fat does not usually vary very much from year to year. The War years were exceptional, since by 1918 the price of seal oil had risen to three or four times the normal

figure. Although the catches of seals in 1916, 1917 and 1918 were not particularly good (indeed 1918 was rather a poor year), their value was enormous, reaching $863,553 in 1918, when the men's share averaged $140 each. (The men's share is one-third of the total value, divided equally among them. This is done ship by ship, so that if a vessel comes back "clean", the men in that ship will get nothing whatever for their 6 weeks' work.) During the War, Newfoundland enjoyed prosperity such as it has never known before or since.

After the War there was a series of poor seal fisheries, below 140,000 from 1919 to 1925 inclusive. Since 1925, however, the number has fallen below this figure on only two occasions, in 1931 and 1932.

Fig. 8 shows smoothed curves (5-year means) for the number of seals brought in, for the number of men, and for the number of seals per man, on the same scales as in Figs. 2, 3, 4. Certain features are now apparent which the unsmoothed figures do not show. The upward trend of the "seals per man"

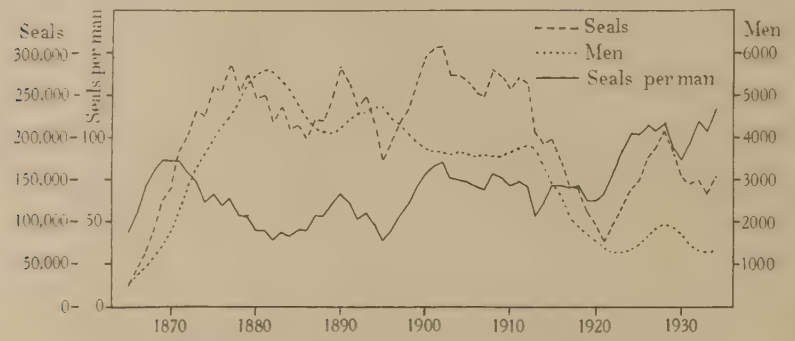

Fig. 8. Smoothed curves (5-year means), showing number of seals brought in, number of men sealing, and number of seals per man.

curve is on the whole more obvious; but even after smoothing, this curve and that for "seals" show large fluctuations. Perhaps the most striking result is seen when the curve for "number of men" is compared with that of "seals per man" (in Fig. 8).

In the early years, while the steam fishery was new and to some extent experimental, each year attracted more men, and they caught more and more seals each. By 1870, as has been mentioned, the steam fishery was established, though for the next 10 years more and more men joined the steamers. During the whole of this decade, however, the number of seals per man steadily decreased from about 85 to about 40. After 1881, however, the number of men decreased steadily till 1889; but this decrease was followed in a year or two by an increase in the seals caught per man. By 1890 more men were again fishing, and again, after a lag of a year or two, the number caught per man decreased. From 1895 to 1901 the number of men again decreased, with a corresponding increase a year later in the number of seals per man. From 1901 to 1914 the

number of men remained roughly constant with a slight tendency to increase, while the number of seals caught per man slowly fell off.

Then came the five or six peculiar years covering the Great War. The number of men fell off for various reasons, such as overseas service and the partial scattering of the fleet and, as might be expected, the number of seals caught also decreased greatly. But the number caught per man remained roughly constant, and this is the only period during the 70 years under review in which a decrease in the number of men was not quickly followed by an increased catch per man. Since 1920 this relationship has been re-established. The number of men has remained low (below 2000) while the number of seals per man has greatly increased; the latter figure has increased most rapidly when the number of men has been declining or at minimum (viz. 1920–4 and 1930 onwards) and after the number of men rose to a small peak around 1928 the catch per man fell off for a year or two.

For 40 years before the War, and also since 1920, there has been a remarkable correspondence between the total number of seals caught and the number caught per man. In other words the "total seals" and "men" curves show much the same inverse relationship as that described in the previous paragraph for "seals per man" and "men", implying that, under some conditions, the more men out hunting the fewer seals do they catch altogether. This is not always true of course, and within wide limits does not apply at all. For example, since 1920 the number of men has been below 2000, and the number of seals has averaged about 150,000, whereas before the War the number of men varied between about 3000 and about 6000, while the catch averaged about 230,000.

When the occasions are examined when the number of men was at a maximum, the reverse is true. The first "seals" peak occurred around 1877, when the men numbered some 4500: but the latter increased to some 5600 by 1881, while the seals caught decreased by some 30,000, and continued to diminish by another 50,000 by 1886. Meanwhile the number of men had again fallen to about 4500, upon which the seals again increased by 80,000 in 5 years. So soon as the men, after a minimum of about 4100 in 1889, numbered 4300 once more, however, the number of seals fell off, and reached a minimum around 1895 corresponding to a maximum number of men at the same time. Then for 8 years the men became fewer while the number of seals caught increased, until a rude balance was struck which lasted up to the War, about 3600 men capturing some 270,000 seals each year, or about 75 per man.

How long this would have gone on it is, of course, impossible to say, but it is not easy to see any evidence during this period which shows that the seals were being overfished, except perhaps the fact that the number caught per man failed to rise when the number of men decreased so markedly during the War. Since 1920 there has been no lack of seals, and at the present time there is nothing to show that the seals are being seriously diminished in number.

The occasions in the last century, however, when the number of men increased towards a maximum with a resultant decline in the total number of seals caught, do show that it is possible to overfish the seals, and that the danger limit appears to lie in the region of 4000 men.

From an ecological point of view, it is comforting to reflect that, since a ship is always accustomed to carry a full crew, a decreased catch per man means decreased profit to the owner of the ship. As soon as the seals have decreased sufficiently it is no longer profitable to run so many ships, and the number of men automatically decreases. This lessens the pressure on the seal herds, and their numbers (and the number of seals killed) increase once more.

The most remarkable aspect of this sequence of events is, perhaps, the rapidity with which the seal herds recover. They are slow breeders, producing but one young one each year and taking 4 years to grow up, yet their fluctuations appear to follow those of the men hunting them by only a year or two. This seems to be good indirect evidence that there is somewhere an enormous reservoir of breeding seals, only a small proportion of which come down each year to the waters off Newfoundland.

The position at the present time then appears to be one of no danger. Should the hypothetical reservoir become diminished for any reason, however, a very different situation might arise. The industry needs careful watching, therefore, and it is hoped that the present paper, if kept up to date by those interested, may afford some guide as to state of the seal fishery from time to time.

Finally, since the seals are only holding their own and are showing no signs of returning soon to their former abundance, a suggestion to the industry might not be considered altogether out of place. If the seals were to be left entirely alone for, say, 10 years, or the catch limited to 100,000, there is little doubt that their numbers would increase faster than they appear to be doing at present. Once the herds are larger, it will be possible to kill more seals without risk of depopulation, and so increase profits in the long run. Any such policy would need very careful watching and control, but as almost the entire seal industry is in the hands of two firms, there should not be any serious difficulty in carrying it out.

7. Summary

1. The seals hunted off Newfoundland belong to two species: the "harps", *Phoca groenlandica*, and the "hoods", *Cystophora cristata*. The harps usually make up about nine-tenths of the total catch.

2. The intensive schooner fishery in the second quarter of the nineteenth century considerably reduced the seal population.

3. Steamers were introduced in 1863 on account of their greater ability to penetrate the ice, seals being less easy to come at than formerly.

4. During the War the large sealing fleet was scattered, and only a small remnant has been in use since.

5. The success or otherwise of the seal fishery in any one year depends partly on a large number of unpredictable and highly variable factors both meteorological and hydrographic. The most important single factor, however, is the number of men hunting the seals.

6. Since the War this number has been comparatively small, and the catches have also on the whole been smaller than before the War.

7. The number of seals caught per man, however, has tended to increase. This seems to show that the seal herds are, at the present rate of fishing, not decreasing, and that they may be actually increasing again slowly, though they are still far smaller than they were before 1850.

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NOTES ON SOME ANIMAL COMMUNITIES OF NORWEGIAN LAPLAND

AN ACCOUNT OF THE DUNG AND CARRION COMMUNITIES AND OF THOSE INSECTS FOUND IN HUMAN DWELLINGS

By J. E. DUFFIELD

(*With Plate* 6)

1. Introduction

The ecology of an area can best be studied by a preliminary biological survey followed by a more intensive study of the different ecological communities. This paper cannot be called a preliminary survey, it is but a first step. It is the result of a traverse of Norwegian Lapland during the Oxford University Lapland Expedition in 1930, during which it was not possible to remain in one locality long enough for anything more than a very cursory investigation of the fauna to be made. The author concentrated on a few of the better defined communities rather than on obtaining an extensive collection, for the Arctic fauna is too well known from the systematic viewpoint to justify the latter course.

In investigating an area time must inevitably be spent in groping before the different animal communities separate out and the principal actors in them become apparent. It is indeed impossible to proceed far beyond this somewhat bewildering stage until the specimens are named. This paper is intended to give subsequent workers an idea of some of the species to expect in the communities discussed.

Where such are available, data on numbers have been included; figures indicate the number of specimens in the collection from that locality. Generally they may be taken as an approximate guide to the relative numbers at that particular time; but it was impracticable to collect all the members of even small communities, and of those collected some of the more fragile, such as the Diptera, were damaged, so too much stress cannot be laid upon the figures. By "a few = F" is meant less than ten and more than three, and by "abundant = A" more than twenty. Below the first section a brief account of the localities is given, and below the other two sections such additional information as seemed necessary.

A short account of the Expedition has been published by Elton (1931), and for a description of the vegetation the article by Leach & Polunin (1932) should be consulted.

The author's thanks are due to all members of the Expedition: without their help the lists would have been considerably shorter. In particular the author wishes to thank Mr Charles Elton for his help in the field in Lapland

Phot. 1. Open birch wood near Goeidnovuoppe camp, 28 July 1930. Vegetation beneath birches is *Empetrum nigrum* (va-d), *Vaccinium myrtillus* (a), *V. vitis-idaea* (f-a), *V. uliginosum* (f-o), *Deschampsia flexuosa* (f), *Betula nana* (o), *Juniperus communis* (o).

Phot. 2. General view of Sjusjavrre, between Beskenjarrga and Goeidnovuoppe, taken 22 July 1930. Typical Lapp village.

and for much useful advice subsequently. Acknowledgement is also due to the following specialists for naming the various groups: Messrs K. G. Blair (Coleoptera); M. Cameron (Staphylinidae); J. M. Brown (Collembola); W. E. China (Hemiptera); J. E. Collin (Diptera); H. St J. Donisthorpe (Formicidae); F. W. Edwards (Diptera); Dr R. Hanitsch (Blattidae), and Dr A. R. Jackson (Araneidae). The author also wishes to thank Prof. G. Hale Carpenter for allowing him the use of the Hope Department at Oxford, where the collections now are; and Dr B. M. Hobby for advice on arranging the lists of insects.

2. Localities

Lakselv (*Finmark*). A village of about a dozen houses at the foot of the Porsanger Fjord and about 20 miles from the coast. It is slightly north of 70° N. lat. and about 80 ft. above sea-level. In and around the village is grass cropped close by animals; beyond is open birchwood (*Betula odorata*) country. A river runs through the village. In and around the village are many "collections" of horse and cow dung where the animals congregate, and it was from these that most of the collecting was done. In all, two working days were spent collecting and probably most of the commoner species of the dung communities were taken. Twenty-two species[1] were recorded altogether. It was early July and the weather was warm and sunny.

Kolvik (*Finmark*). A village some 4 miles north of Lakselv and on the coast of the Porsanger Fjord. The country round is much like that at Lakselv, and domestic animals are plentiful, nine species were taken. Only 2 hours on 9 July were spent collecting. Weather warm and sunny.

Billefjordelv (*Finmark*). This is the name of a river. Collecting was done in the *Betula odorata* zone some 5 miles west of Kolvik. The country consists of hills and river valleys, and there are few animals in it except some sheep. Dung was scarce and only 1 species was recorded. Average elevation was about 600 ft. Three days (10, 11 and 12 July) were spent there; all were hot and sunny.

Karasjok (*Finmark*). A town some 30 miles south of the foot of the Porsanger Fjord. It is situated on a river about 400 ft. above sea-level. In and around the town are cropped grassland and some hay fields, while along the river valley are pines (*Pinus sylvestris*) and a few birch (*Betula odorata*); away from the valleys open birchwood replaces pine. Domestic animals are plentiful. Ten species were taken in a day and a half (16 and 17 July); the weather was cool and showery with fine intervals.

Beskenjarrga (*Finmark*). A village 8 miles south-west of Karasjok and on a river. The surrounding country is open birchwood and there are some cows and a few horses in the locality. The elevation is about 450 ft. One day (19 July) was spent collecting and 12 species were taken. The weather was cool and dull; there had been rain during the previous night.

Goeidnovuoppe (*Finmark*). A small village on the Kautokeino River and

[1] These are the numbers of dung species.

Table 1. *Dung communities*

Species found in dung	Localities									
	Lakselv	Kolvik	Billefjordelv	Karasjok	Besken-jarrga	Goeid-novuoppe	Mieron	Ladnatj-avrre	Bossekop	Punta
ARANEIDA										
Erigone arctica White	–	–	–	–	–	–	–	–	+	–
Lycosa tarsalis Thor.	+	–	–	–	+	–	–	–	–	–
Mitopus morio Fabr.	–	+	–	–	–	–	–	–	–	–
Tarentula aculeata Clerck	–	–	–	–	–	+	–	–	–	–
COLEOPTERA										
Carabaeidae										
Nebria gyllenhali Schon.	–	–	–	–	+(1)	–	–	–	–	–
Chrysomelidae										
Chrysomela marginata L.	+(1)	–	–	–	–	–	–	–	–	–
Cryptophagidae										
Cryptopleurum minutum F.	+(A)	–	–	+	+(A)	–	+(A)	–	–	+
Elateridae										
Hypnoidus rivularis Gyll.	+(8)	–	–	–	–	–	–	–	–	–
Hydrophilidae										
Cercyon melanocephalus L.	+(A)	+(A)	–	+(A)	+(A)	–	+(A)	–	+(A)	–
C. unipunctatus L.	–	–	–	+(3)	–	–	–	–	–	
Lathridiidae										
Enicmus minutus L.	–	–	–	–	–	–	+(1)	–	–	–
Scarabaeidae										
Aphodius borealis Gyll.	–	+(A)	–	–	–	–	–	–	–	–
A. lapponum Gyll.	+(A)	+(A)	–	–	–	+(A)	+(A)	–	+(A)	+
A. piceus Gyll.	–	+(A)	–	–	–	–	+(1)	+(A)	+(A)	–
A. putridus Hbst.	–	+(A)	–	–	–	–	+(A)	–	+(A)	+
Silphidae										
Thanatophilus lapponicus Hbst.	–	–	+(2)	–	–	–	–	–	–	–
Staphylinidae										
Aleochara bilineata Gyll.	–	–	–	–	–	–	–	–	+(F)	–
A. diversa Sahlb.	–	–	–	–	–	–	+(F)	–	–	–
A. moerens Gyll.	–	–	–	–	–	–	–	+(F)	–	–
Atheta atramentaria Gyll.	+(A)	–	–	+(A)	+(A)	+(A)	+(A)	+(A)	+(A)	+
A. fungi Gr.	+(1)	–	–	–	–	–	–	–	–	–
A. longicornis Gr.	–	–	–	–	+(1)	–	–	–	+(1)	–
A. setigera Sh.	–	–	–	–	–	–	–	–	–	+
Autalia puncticollis Shp.	–	–	–	–	–	–	–	–	+(1)	–
Deliphrum tectum Pk.	–	–	–	+(2)	–	+(2)	+(2)	+(1)	–	–
Haploderus caelatus Gr.	–	–	–	–	–	–	–	–	+(6)	+
Oxypoda opaca Gr.	+(A)	–	–	+(A)	+(A)	–	+(A)	–	+(A)	–
Oxytelus laqueatus Marsh.	+(A)	–	–	–	–	+(A)	+(A)	+(A)	–	+

| | | |

50 miles south-west of Karasjok. The altitude is about 900 ft. The surrounding country is open birchwood, and there are a few domestic animals in the locality. Only 7 species were taken from dung. Eight days (24 to 31 July) were spent collecting. On the whole the weather was fine and cool, but there were periods of rain.

Mieron (*Finmark*). A village on the Kautokeino River 5 miles south-west of Goeidnovuoppe. The country is similar to that at Goeidnovuoppe, but there are more domestic animals about the village. Elevation is about 950 ft. Six days (1–6 August) were spent collecting and 15 species were found. The weather was fine, warm and mostly sunny.

Ladnatjavrre (*Finmark*). A hut by the river. Post-horses stop in the clearing around the hut, and hence there was plenty of dung. The vegetation round the hut is more dense than at the previous localities. One day (7 August) was spent collecting and 6 species were found. The weather was fine and hot.

Bossekop (*Finmark*). A town near Alta on the north-west coast. This is the only locality in which we found well-developed pinewoods (*Pinus sylvestris*), and these had been considerably damaged by cutting for some distance around the town. There was a moderate amount of horse and cow dung on the outskirts of the town and in the pinewoods. One day (9 August) was spent collecting and 15 species were found. The weather was fine and hot.

Immerfoss (*Troms*). A waterfall forming the head of river-boat navigation in the Reisendal. It lies in a deep gorge, with pine, birch and alder woods. Height not shown on map. About 40 miles from the valley entrance at the coast. Collections made on 11 and 12 August. Cold but sunny.

Punta (*Troms*). A scattered farming settlement in the central part of Reisendal, with pine and birch woods, and hay meadows among the river flats. Collections made on 18 August (carrion) and 19 August (dung). 13 species.

3. Dung communities (see Table 1)

Conclusions. It appears that the average number of species found in a dung community is about 12. By a "dung community" is meant a collection of droppings of different ages and in such proximity that any insect may pass readily from one to another. At Lakselv a typical example was seen where the cattle congregated in the middle of the village while waiting to be milked. Except for Billefjordelv, every locality had at least one such community. Billefjordelv was a region in which there were only occasional droppings from roaming animals (cattle, reindeer and horses). Thus although a day and a half were spent collecting there only 1 species was discovered, for food was evidently too scarce for a larger population to survive. There was not time on this expedition to estimate the total populations of individual droppings or communities, but there would be no great inherent difficulties in doing this.

The insects seem to fall into four main categories. First, those which are widely distributed and plentiful of which the following are examples: *Aphodius*

lapponum, *A. piceus*, *Atheta atramentaria*, *Cercyon melanocephalus*, *Cryptopleurum atomarium*, *Oxypoda opaca*, *Oxytelus laqueatus*, and the flies *Limosina* spp. and *Scatophaga suilla*. Secondly, those which are fairly plentiful but local, such as *Cercyon unipunctatus*, *Haploderus caelatus*, *Hypnoidus rivularis*, *Philonthus scoticus*, *Tachinus rufipes*, *Oscinus frit*. Thirdly, species which are widely distributed but occur in small numbers, such as *Deliphrum tectum* and *Platystethus arenarius*. Fourthly, a large group of casual visitors to dung, such as *Formica fusca*, *Chrysomela marginata*, *Nebria gyllenhali*, *Tachyporus jocosus*, the Araneidae, and others. Further work would undoubtedly greatly modify the list of species within each group, but the author believes the division to be valid.

As to the relation of certain species to different ecological zones it is noteworthy that more species of *Aphodius* were found at the two coastal towns, Kolvik and Bossekop, than inland, although less than 2 days were spent collecting on the coast. It will be seen that several species are recorded from only one locality, but the data are too meagre to justify any speculation on this subject.

The species of Diptera collected numbered 13 and were in addition few in individuals, whereas the Coleoptera were more numerous in individuals and 36 species were taken. Allowance must be made for the smaller number of Diptera reaching England in an identifiable condition (all specimens were wrapped in screws of paper and carried in a cigar box in a rucksack) but even so a comparison with the relative numbers of the two groups taken from carrion shows a reversal of the above proportions.

4. CARRION

The following is a list of species found on carrion at Goeidnovuoppe in mid July. The carrion (bodies of voles that had been trapped) was about four days old and the weather was warm with some rain. No attempt was made to study the succession of insects as decay progressed. The species of voles were *Microtus ratticeps*, *Evotomys rutilus* and *E. rufocanus*.

COLEOPTERA
- Carabaeidae
  - *Bembidium velox* L. var. *lapponicum* Thoms. (F)
- Scarabaeidae
  - *Aphodius piceus* Gyll.
- Staphylinidae
  - *Atheta atramentaria* Gyll. (A)

COLLEMBOLA
- *Hypogastrura armata* (Nic.)

DIPTERA
- Anthomyidae
  - *Helina luteisquama* Zett.
  - *Hydrotaea dentipes* F.
  - *H. occulta* Mg.
  - *Hylemyza lasciva* Zett.
  - *Orthellia caesarion* Mg.
  - *Paregle radicum* L. (A)
  - *Pogonomyia decolor* Fln.
- Cordyluridae
  - *Piophila calceata* Duda
  - *P. luteata* Hal. var.
  - *P. varipes* Mg.
  - *P. vulgaris* Fln.
  - *Scatophaga suilla* F.
- Helomyzidae
  - *Leria septentrionalis* Collin
- Muscidae
  - *Calliphora uralensis* Vill.
  - *Mesembrina mystacea* L.
  - *Morellia hortorum* Fln.
  - *Myiospila meditabunda* F.
- Sepsidae
  - *Nemopoda pectinulata* Lw.
  - *Sepsis orthocnemis* Frey.
- Tachinidae
  - *Lucilia* ? *caesar* Zett.

HEMIPTERA HETEROPTERA
- *Aradus lugubris* Fall.

In addition J. M. Weatherby collected from a recently shot bird in this locality a single specimen of the fly *Ornithomyia lagopodis* Shp. This was also found by T. H. Harrisson on a blue-throat (*Luscinia suecica*) at Immerfoss, 12 August.

At Mieron three specimens of the beetle *Thanatophilus lapponicus* Hbst. were found under a dead pike *Esox lucius*; also some specimens of the fly *Leria septentrionalis* Collin.

Charles Elton supplies the following notes: At Immerfoss, the fly, *Paregle radicum* L., was found on the guts of a red-backed vole (*Clethrionomys*) which some bird of prey had left on rocks by the river. Numbers of another fly, *Piophila vulgaris* Fln., were just emerging from pupae in the body of a rough-legged buzzard (*Buteo lagopus*) in the same place. Next day these flies were copulating on the carcase.

A fly, *Aphiochaeta humeralis* Zett., and an ant, *Camponotus herculaneus* L., were taken on the carcases of voles in traps at Punta; here also another ant, *Myrmica lobicornis* Nyl., was found on the skinned body of a mouse left in a pasture field.

Conclusions. It will be seen that of the 30 species recorded, no less than 22 are Diptera, and of these only 6 species are recorded from the dung communities. In contrast to the dung, Staphylinid beetles are remarkable for their scarcity.

5. Insects found in and around human dwellings

Below is given a list of species recorded from huts, hotels and earth closets. It may be of interest to compare it with the lists in the two previous sections; and with one giving lists of insects found in the birch woods away from habitations which the author hopes to publish later.

From a wooden Lapp hut, overcrowded with children, at Goeidnovuoppe, mid July:

Diptera
- *Fannia canicularis* L.
- Mosquitoes (unnamed)
- *Simulium* sp.

Hemiptera heteroptera
- *Aradus lugubris* Fall.

From a small wooden hut near Mieron in which three men had slept the previous night, end of July:

Diptera
- *Hydrotaea dentipes* F.
- Mosquitoes (unnamed)
- *Musca domestica* L.
- *Oscinis frit* L. var. *vastator* Curt.
- *Pogonomyia decolor* Fln.

Hemiptera heteroptera
- *Aradus lugubris* Fall.

From a hut at Mieron, late July and early August:

Diptera
- *Anisopus fenestralis* Scop.
- *Cynomyia mortuorum* L.
- Mosquitoes (unnamed)
- *Phormia groenlandica* Zett.
- *Pogonomyia decolor* Fln.
- *Rhadiurgus variabilis* Zett.
- *Simulium* (unnamed)

Diptera (*cont.*)
- *Stomoxys calcitrans* L.
- *Tipula pseudocinerascens* Strobl.

Hymenoptera
- *Formica fusca* L.

Trichoptera
- *Molanna augustata* Curt.

From an earth closet (very insanitary) 60 ft. from the hut at Mieron, end of July and early August:

ARANEIDAE
Mitopus morio Fabr.
DIPTERA
Leria pleuralis Beck.
L. serrata L. (*in coitu*)

From the window of a small, dark hut at Ladnatjavrre in which two men had slept the previous night, early August:

COLEOPTERA
Nitidula bipunctata L.
DIPTERA
Diazosma hirtipenne Siebke
Mydaea orichalcea Zett.
Pegohylemyia cf. *discreta* Mg.
Pegomyia sp.
Phaonia hybrida Schnbl.
Protocalliphora azuria Fln.

From a small hotel at Bossekop, 9 August:

DIPTERA
Calliphora erythrocephala Mg.
Fucellia fucorum Fln.
Leria modesta Mg.
Muscina stabulans Fln.

From the water closet of the same hotel, 9 August:

ARANEIDAE
Stearodea bipunctata L.
DIPTERA
Fannia scalaris F.
Scoliocentra villosa Mg.

Conclusions. As one would expect, Diptera are by far the most abundant order in the above list; they account for 28 out of the 34 listed species. No attempt has in most cases been made to indicate the abundance of the different species: so many arrived in an unidentifiable condition that it would be useless to do so. The two groups remarkable for their abundance were the mosquitoes and the Simuliid flies, both of which were taken in such quantities that no specialist would undertake their identification. It is probable that only a few different species were represented in these groups. As with the dung insects, many species were taken from one locality only, but the collection is not sufficiently extensive to suggest that any species is confined to a given locality. However, it is interesting to note that the common English species, *Musca domestica*, is recorded from Mieron alone. The author was surprised to find that only one species, *Pogonomyia decolor*, occurred in all three of the habitats discussed. *Oscinis frit* was the only other species which was found on dung and in houses, and *Hydrotaea dentipes* was the only additional species recorded from carrion and houses. It is also interesting to see that none of those species taken in earth closets is recorded from dwelling houses, although there was apparently no barrier other than preference which prevented free interchange between the two habitats.

6. Summary

These notes, made in the course of a traverse of Norwegian Lapland, during the Oxford University Lapland Expedition, 1930, show that there are well-defined animal communities of dung and of carrion, with few species in common. Lists from various localities and sub-habitats are given. Fifty-eight species were found on and in dung, 30 on and in carrion, and 34 in human dwellings.

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AN ECOLOGICAL STUDY OF A THRIPS (*APTINOTHRIPS RUFUS*) AND ITS NEMATODE PARASITE (*ANGUILLULINA APTINI*)

By AVERIL M. LYSAGHT

(*With 7 Figures in the Text*)

CONTENTS

	PAGE
1. Introduction	169
(*a*) Outline of problem	169
(*b*) Description of the grass plots	170
(1) Manurial treatments	170
(2) Chemical data	171
(3) Botanical data	172
(*c*) Technique	173
(1) Sampling	173
(2) Culturing the nematode	174
2. Biology of the nematode	174
(*a*) Life cycle	174
(*b*) Experimental work	177
(*c*) Seasonal variation in abundance of the nematode	178
(1) Effect of temperature	178
(2) Effect of rainfall	180
(3) Total numbers of parasite and host	180
(*d*) Morphological effect of parasite on host	182
3. Variation in numbers of host insect	183
(*a*) Evidence	183
(*b*) Effect of parasitism	184
4. Difference in percentage parasitism on eleven plots	186
(*a*) Evidence	186
(*b*) Chemical factors	188
(*c*) Botanical factors	188
(1) Experiments	188
(2) Discussion	190
(*d*) Parasites other than the nematode	191
5. Discussion	191
6. Summary	191
References	192

1. Introduction

(*a*) *Outline of problem*

It is almost a century now since scientists began to set out long-term experiments to elucidate the causes of differences in vegetation such as occur, for example, in the clearly defined zones on mountain slopes. The classical fields

at Rothamsted are valuable from this point of view. In 1856 the meadowland which comprises Park Grass was divided into strips for experimental work on the effect of fertilizers on grassland. Since then the plots have undergone differential manurial treatments and have been annually cropped for hay. Differences in the vegetation and sometimes in the insect population of these plots have become apparent. The present investigation was undertaken in order to determine, if possible, what factors influenced the distribution of the parasites of an insect which occurs on all the plots.

A wingless Thysanopteron, *Aptinothrips rufus* Gmelin, is abundant throughout the year on the grasslands at Rothamsted. It is parasitized by a nematode *Anguillulina aptini* (Sharga). Sharga (unpublished observation), working on samples from two of the plots, found that the parasite was apparently absent from one although common on the other. The two plots have had similar manurial treatment except that one has been dressed with lime while the other has not.

In 1933–5 observations concerning the distribution of both the host and parasite on eleven of the plots were made at intervals to see whether the difference in abundance of the parasite was significant or fortuitous.

I wish to thank Sir John Russell for his kindness in allowing me to work at Rothamsted Experimental Station. The investigation was carried out in the Entomology Department under the stimulating direction of Dr C. B. Williams. To him and to the other members of the staff who have discussed the questions involved and who have been generous with helpful criticism I am most grateful. Thanks are also due to Mr Samuel and Mr Moore who kindly undertook the culture of a fungus parasite of *Aptinothrips rufus*, to Mr P. Simon, without whose assistance the experiments involving water cultures and the growing of a number of grasses could not have been carried out, and to Messrs Sutton and Son who supplied varieties of grass seed for experimental purposes.

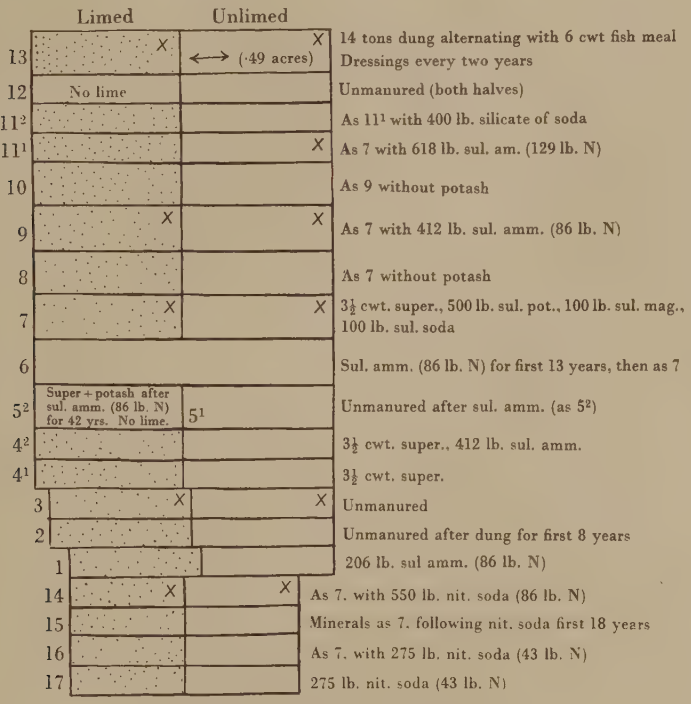
(*b*) *Description of the grass plots*

(1) *Manurial treatments*

The material from which the insects were collected for examination was obtained by sampling a number of plots from the field called Park Grass. This field was divided into plots for experimental purposes in 1856 (Lawes & Gilbert, 1880 1900). The plots used in the present investigation were chosen so as to give as great a range as possible of manurial treatment and of resultant variation in the herbage. They vary in size from one-half to one-twelfth of an acre. Their relative positions and treatments are shown in Fig. 1. Each plot is divided into two halves, similarly treated save that the south-west half of each has been limed regularly since 1883, and the other half left unlimed. No lime was applied at all before that year.

(2) *Chemical data*

Recent data on chemical analyses of the soils have been kindly supplied by the Chemistry Department and are given in Table 1: the plots differ considerably and present a wide range of *p*H values.


Limed
Unlimed
13
14 tons dung alternating with 6 cwt fish meal
Dressings every two years
(·49 acres)
12
No lime
Unmanured (both halves)
11²
As 11¹ with 400 lb. silicate of soda
11¹
As 7 with 618 lb. sul. am. (129 lb. N)
10
As 9 without potash
9
As 7 with 412 lb. sul. amm. (86 lb. N)
8
As 7 without potash
7
3½ cwt. super., 500 lb. sul. pot., 100 lb. sul. mag., 100 lb. sul. soda
6
Sul. amm. (86 lb. N) for first 13 years, then as 7
5²
Super + potash after sul. amm. (86 lb. N) for 42 yrs. No lime.
5¹
Unmanured after sul. amm. (as 5²)
4²
3½ cwt. super., 412 lb. sul. amm.
4¹
3½ cwt. super.
3
Unmanured
2
Unmanured after dung for first 8 years
1
206 lb. sul amm. (86 lb. N)
14
As 7. with 550 lb. nit. soda (86 lb. N)
15
Minerals as 7. following nit. soda first 18 years
16
As 7. with 275 lb. nit. soda (43 lb. N)
17
275 lb. nit. soda (43 lb. N)

"X" indicates that a plot has been sampled for *Aptinothrips rufus*

Fig. 1.

Table 1

Plot...	3 L	3 U	7 L	7 U	13 L	13 U	9 L	9 U	14 L	14 U	11¹ U
A	7·3	5·6	6·7	5·1	6·6	4·7	5·0	4·0	7·2	6·0	3·8 (1923)
B	94	4	109	0	99	30	21	−1	108	105	—
C	24	25	32	39	45	32	28	34	38	40	—
D	—	1·51	1·20	1·31	1·09	1·18	1·09	1·37	1·07	1·07	—
E	—	0·18	0·43	0·41	0·55	0·61	0·68	0·77	0·55	0·60	—

U = unlimed plot. L = limed plot.
A = *p*H values for 1933, 2 years after liming.
B = percentage nitrification (1933).
C = average mineralizable nitrogen (1933).
D = percentage nitrogen in herbage (hay (1931), with 80 % dry matter).
E = cwt. nitrogen per acre in hay (1931).

Data for 11[1] U are not given here as it has not been subjected to chemical or botanical analysis since 1924 and it was not included in the present investigation till 1934. Its herbage is almost identical with that of 9 U but its *p*H value is slightly lower (3·8 in 1923).

An attempt was made to correlate these and other values with the percentage infection of *Aptinothrips rufus* both by the nematode and by a parasitic fungus (Lysaght, 1936 *b*). None of the correlations was significant and certain factors were thus eliminated.

(3) *Botanical data*

Unfortunately an exact botanical analysis of the plots is not available. The most recent was published by Brenchley in 1924 since when considerable changes have taken place. At that time the main constituents of the herbage on 9 U were *Agrostis vulgaris*, *Anthoxanthum odoratum*, *Arrhenatherum avenaceum*, *Festuca ovina*, *Holcus lanatus*, *Dactylis glomerata* and *Rumex*

Table 2

Limed	Unlimed
	Plot 3
Avena pubescens	*Avena pubescens*
Briza media	*Briza media*
Dactylis glomerata	*Anthoxanthum odoratum*
Anthoxanthum odoratum	*Festuca ovina*
Festuca ovina	*Conopodium denudatum*
Poa pratensis	
Trifolium pratense (v. ab.)	
Ranunculus acris	
	Plot 7
Avena pubescens	*Avena pubescens*
Anthoxanthum odoratum	*Anthoxanthum odoratum*
Dactylis glomerata	*Dactylis glomerata*
Briza media	*Briza media*
Taraxacum officinale (v. ab.)	*Trifolium pratense*
	Conopodium denudatum
	Alopecurus pratensis
	Poa pratensis
	Plot 9
Holcus lanatus	*Holcus lanatus* (v. ab.)
Anthoxanthum odoratum	*Anthoxanthum odoratum* (sc.)
Alopecurus pratensis	
Bromus mollis	
Poa pratensis	
	Plot 11[1] U
	Holcus lanatus
	Plot 13
Alopecurus pratensis	*Alopecurus pratensis* (v. ab.)
Dactylis glomerata	*Dactylis glomerata* (sc.)
Arrhenatherum avenaceum	*Arrhenatherum avenaceum* (sc.)
Holcus lanatus	*Conopodium denudatum* (sc.)
	Rumex acetosa (sc.)
	Plot 14
Arrhenatherum avenaceum	*Arrhenatherum avenaceum* (v. ab.)
Anthoxanthum odoratum	*Alopecurus pratensis*
Dactylis glomerata	*Bromus mollis*
Poa trivialis	*Avena pubescens*
Poa pratensis	

acetosa. In 1928–9 the winter was exceptionally hard and the only grass able to withstand both the extreme cold and the high acid content of the soil was *Holcus lanatus*. This plot is now almost covered with *H. lanatus* but there is a little *Anthoxanthum odoratum* as well. Plot 11^1 U is rather similar but even in 1924 *Holcus lanatus* was dominant. Occasionally *Anthoxanthum avenaceum* has been plentiful and a few other species could always be found. Now however *Holcus lanatus* makes up the entire herbage and the surface is a thick peaty mat.

The growth on 9 U and 11^1 U is coarse and rank. The latter yields a heavier crop of hay than any other in this series. It produces on an average 58 cwt. per acre from the first cut while the rest yield from 11 to 52 cwt. The herbage on all the other plots consists of a number of species, and though sometimes one may be particularly abundant, in no case does it dominate the rest of the association. A list of the commoner species which were in flower in May and June 1933 is given in Table 2. It is by no means complete but is compiled from eye observations carried out by the Botany Department.

(*c*) *Technique*

(1) *Sampling*

Samples were taken at intervals of about one week throughout the spring and summer of 1933. In 1934 they were taken weekly from February till November, and then at intervals of from 2 to 3 weeks until the end of February 1935. As the grass was cut on each plot it was put into paper bags and then brought back to the laboratory for examination. Each sample was left in a large glass jar covered with muslin until I was ready to work through it (not more than 3 or 4 days).

Aptinothrips rufus is about 1·25 mm. in length, wingless, and yellowish brown as its name denotes. It can be distinguished quite easily from the other thrips found with it since it is more slender than the pale larval forms of the commoner winged species and has a peculiar gait. Specimens were at first collected with a camel-hair brush but later an aspirator was used. Various methods were used for killing the insects, but anaesthetizing with chloroform proved to be the most satisfactory. If, however, too much vapour were present the blood coagulated rapidly and the parasites degenerated almost immediately. A simple device was suggested to me and proved effective. A wide-necked bottle of chloroform was fitted with a rubber cork in which two holes were bored. The glass tubing from the bottom of the aspirator containing the thrips was fitted through one hole, while through the other was passed a piece of bent glass tubing to which a rubber bulb was attached. Pressure on the bulb forced chloroform vapour up through the aspirator and in this way a very small amount could be used.

Dissections were made in Ringer's solution. Centrifuging of washings from the grass of a heavily infested plot were carried out in the summer of 1934 in

the hope of finding the free-living stages of *Anguillulina aptini*, but the only nematodes collected were free-living and saprophytic forms.

(2) *Culturing the nematode*

The fact that Glaser (1932) and Lapage (1933 *a*) successfully cultivated two widely different types of nematodes suggested that it might be possible to obtain cultures of *A. aptini*. Attempts were made to do this using Glaser's technique. The nematodes were placed on agar plates inoculated with a heavy suspension of baker's yeast, but none lived for more than 2 days although alive and active at the end of 24 hours.

2. Biology of the Nematode

(*a*) *Life cycle*

The adult female nematode although degenerate in many respects has an extremely efficient reproductive system. One parasitized thrips was found to contain a single female nematode, 111 eggs and 18 newly hatched larvae. Other instances are given in Table 3. I obtained no evidence concerning the length of the egg-laying period in individual females.

Table 3. *Typical infestation of individual thrips. "Male larvae" includes only those which are sufficiently advanced to be recognizable on account of their caudal alae*

Females	Eggs	Larvae	(Male larvae)
2	56	133	29
2	33	122	5
2	84	113	4
3	62	122	1
1	43	125	9
1	111	18	0
1	30	113	1
2	145	9	0

The maximum production of eggs is in the spring during the months of April and May (Fig. 2 and Table 4). From the relationship of the curves showing the average numbers of larvae and eggs in infected thrips in 1933 and in 1934–5 it would appear that the incubation period in the spring is between 3 and 4 weeks. After the middle of May the number of eggs drops appreciably but it rises again at the beginning and at the end of July. The curve then slopes fairly smoothly down and reaches its minimum in December. It fluctuates about a low level throughout the winter months and shows a steady rise in March.

It is possible that the drop in May is due to the fact that the overwintering generation of females has died out and that their progeny have not yet reached maturity. After this period development is probably accelerated by the rise in temperature. That this is so is confirmed by the fact that the numbers of eggs and larvae per infected thrips undergo a progressive decrease from the end of

June onwards in both 1933 and 1934, while, on the other hand, in neither year does the curve showing percentage of infected thrips (Fig. 3) reach its maximum till August and September.

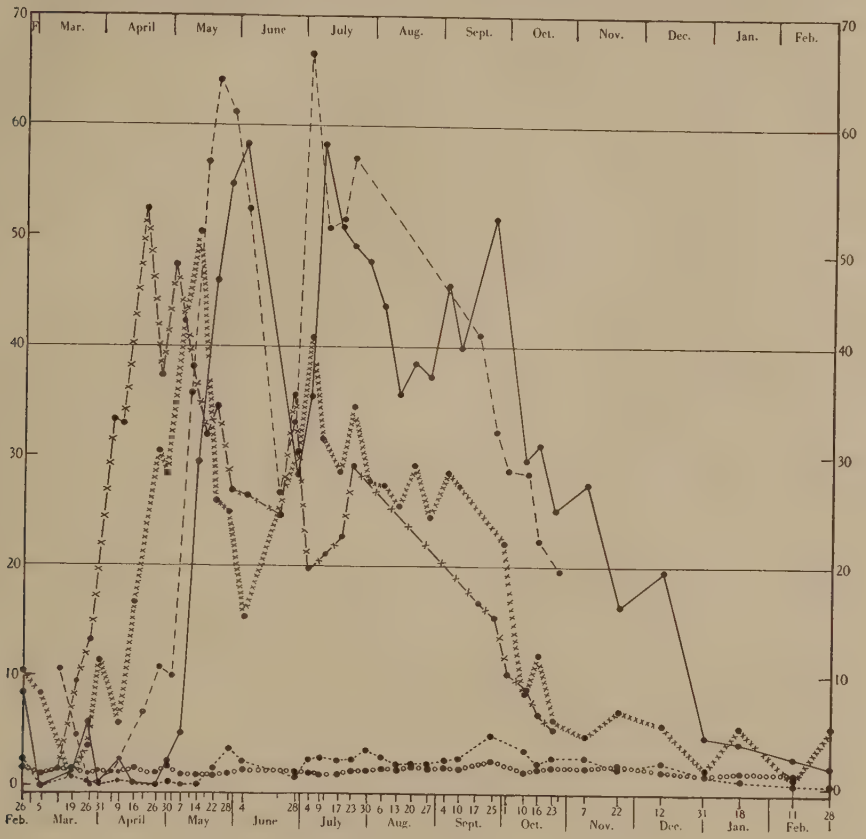


Fig. 2. Average number of nematodes per infected thrips.

	1933	1934–5
Eggs	—x—x—x—	xxxxxxxxxxx
Larvae	— — —	————
Females		ooooooooooo
Male larvae		----------

It is not known whether moulting occurs before the larvae leave the thrips. I think that the young males and females escape from the host early in the morning when the dew is heavy and swim down to the shelter of the grass sheaths and that here moulting occurs and fertilization takes place. On the other hand fertilization may occur in the host before the larvae leave the anus.

Table 4. *Average numbers of nematodes per thrips in weekly samples from all plots*

Date 1933	Number of thrips infected	Average number of nematodes per thrips			
		Males	Females	Eggs	Larvae
13 Mar.	2	2·5	0·0	1·5	10·5
21	11	0·4	0·5	9·6	4·7
27	4	0·0	0·8	13·3	0·0
6 April	8	0·0	0·9	33·5	1·3
10	15	0·0	0·9	32·9	2·5
20	11	0·0	1·2	52·5	6·7
27	9	0·0	1·6	37·2	10·9
2 May	8	0·0	1·0	47·4	10·0
11	17	1·1	1·1	38·1	35·8
18	19	3·2	1·0	32·1	56·8
22	39	4·9	1·3	34·6	64·3
29	27	3·8	1·0	27·0	61·1
5 June	23	2·9	1·5	26·6	52·3
20	23	1·3	1·2	24·7	26·9
26	31	1·3	1·2	35·7	33·2
3 July	55	2·5	1·1	19·9	66·6
11	51	2·5	1·3	21·2	50·8
18	54	2·7	1·4	22·9	51·6
23	60	2·6	1·4	29·3	57·1
18 Sept.	96	2·6	1·9	16·9	41·2
26	47	3·9	1·8	15·5	32·3
2 Oct.	21	3·1	1·9	10·3	28·9
11	18	4·3	3·3	8·9	28·6
16	12	2·3	1·8	6·5	21·3
26	22	2·2	2·0	4·8	19·6
1934					
26 Feb.	5	2·4	1·6	10·2	8·4
5 Mar.	7	0·0	1·0	8·6	0·0
19	6	6·7	1·5	0·8	1·2
26	14	0·3	1·1	3·7	5·8
31	13	0·0	1·5	11·5	0·4
9 Apr.	6	0·3	1·2	5·8	2·3
16	9	0·0	1·6	16·7	0·2
26	19	0·0	1·2	30·5	0·0
30	16	0·4	1·8	28·6	2·1
7 May	20	0·0	1·2	42·4	4·8
14	13	0·0	1·0	50·5	29·5
22	16	1·8	1·1	26·2	45·9
28	20	3·4	1·1	25·1	54·8
4 June	10	2·2	1·2	15·4	58·2
28	20	0·9	1·1	30·4	28·4
4 July	11	2·5	1·5	41·0	37·6
9	23	2·7	1·0	31·8	58·4
17	42	2·6	1·2	28·6	50·7
23	40	2·6	1·3	34·6	49·3
30	41	3·4	1·4	27·8	47·6
6 Aug.	54	2·7	1·7	27·1	43·7
13	65	2·0	1·5	25·5	35·7
20	60	2·2	1·8	29·3	38·6
27	73	2·2	1·8	24·3	37·3
4 Sept.	36	2·5	1·8	28·8	45·3
10	42	2·5	1·7	27·5	40·2
25	44	4·8	2·4	22·1	51·6
10 Oct.	14	3·3	1·4	8·6	29·9
16	28	2·2	1·7	12·1	31·1
23	29	2·8	1·8	6·1	25·2
7 Nov.	22	2·7	1·8	4·7	27·6
22	19	1·7	1·8	7·1	14·4
12 Dec.	15	2·3	1·5	5·7	17·6
31	16	1·1	1·2	1·7	4·5
1935					
18 Jan.	19	0·6	1·5	5·4	4·0
11 Feb.	17	0·4	1·4	0·8	2·8
28	19	0·2	1·2	5·7	2·0

Note. Numbers in the column headed larvae include those which were distinguishable as males as these were thought to be immature.

This hypothesis is supported by the comparatively small number of male larvae which are found throughout the summer (Fig. 2). Males have, however, been found leaving the anus of the host.

After fertilization the female finds a larval or pupal thrips and enters it by means of the stylet which enables it to penetrate the delicate skin of the host. Bovien (1932) has seen females of *Scatonema wülkeri* Bovien penetrating the larvae of *Scatopse fuscipes* Meig. in this way. The female nematode after entering the host loses its worm-like appearance and develops into a swollen sac-like organism in which the reproductive system is the only obvious structure (Lysaght, 1936 *a*).

I think that the last generation of females in the autumn infects the larval thrips which will form the overwintering generation. Development of the female nematodes in these hosts is delayed and few eggs or larvae are found throughout the winter months. The number of females per infected thrips was practically constant during the entire period of sampling. The examination of 1650 infected thrips showed that in the great majority one or two females occurred in each host, but occasionally more were present, up to eight in very rare cases.

Fig. 2 shows the average number of parasites per host insect in 1933 and 1934–5. Numbers of females in 1933 are not shown as the curves for both years are almost identical.

(*b*) *Experimental work*

Experiments were carried out to ascertain whether the life cycle of the nematode could be completed in the absence of soil. Grass seedlings which had been grown in sterilized soil were carefully washed and placed in water cultures. Cellophane cages were fixed over them. Six tubes containing *Holcus lanatus* and six containing mixed grasses were used. The mixed grasses comprised *Agrostis alba*, *Alopecurus pratensis*, *Bromus mollis*, *Dactylis glomerata*, *Festuca ovina* and *Poa pratensis*. Ten thrips from 13 U were placed in each cage. The percentage infection of thrips was 78 % on this plot on 27 August 1934, and 45 % on 4 September, 3 days before this experiment was begun.

The thrips were placed on the mixed grasses on 8 September and on *Holcus lanatus* on 7 September, and were left till 22 October when they were collected for examination. The results are given in Table 5. The cages were left undisturbed during this period, but the solution in the tubes was changed weekly. The grasses did not grow well and in three sets of *H. lanatus* the seedlings died. From the other three 39 thrips were collected. Of these, 35 were larvae, 2 were pupae and 2 adults. One larva only was infested: an immature female was present in its body cavity.

The mixed grasses were much more healthy but only 18 thrips were present, these comprised 4 pupae, 7 larvae and 7 adults. The adults were small and pale. Of these 18, 5 were infected, 4 adults and 1 pupa. This shows that it is possible

(under certain conditions) for the nematodes to complete their life cycle without utilizing the soil. All the available evidence points to the grass sheaths being the habitat of the nematodes in the free-living stage.

Table 5

		Thrips				Nematodes			
Grass		Pupae	Larvae	Adults	Infected specimens	Males	Females	Eggs	Larvae
H. lanatus	(*a*)	—	6	2	1 la.	—	1 (imm.)	—	—
	(*b*)	2	19	—	—	—	—	—	—
	(*c*)	—	10	—	—	—	—	—	—
Mixed	(*a*)	—	—	1	1 ad.	—	2	15	—
	(*b*)	1	1	2	1 pu.	—	2	2	103
		—	—	—	1 ad.	5	2	29	22
	(*c*)	1	—	2	1 ad.	—	1	35	1
	(*d*)	—	—	1	1 ad.	1	1	—	—
	(*e*)	2	3	—	—	—	—	—	—
	(*f*)	—	3	1	—	—	—	—	—

(*c*) *Seasonal variation in abundance of the nematode*

(1) *Effect of temperature*

The graphs for the nine plots seem to exhibit a fairly regular seasonal rhythm. Infection rises gradually in April and May, drops in June, reaches a maximum in August and September and drops at the end of October. In the mild winter of 1934–5 a mid-winter rise occurred on three of the plots, but this did not persist through February. The approximately weekly average of the percentage infection on all the plots for 1934–5 is shown in Table 7 and Fig. 4. The peak was reached on 27 August.

The monthly average of the percentage infection on all the plots in 1933 and 1934–5 is expressed in Table 6 and Fig. 3. The curves for both seasons are almost identical. Samples unfortunately could not be taken in August 1933, and it is probable that infection reached its peak during that month. This would explain the only discrepancy between the curves.

Table 6 and Fig. 3 shows the monthly mean of the minimum temperature on grass and it is obvious that a relationship exists between the rise in temperature and infection.

Correlations were worked out to estimate the significance of this relationship. The average minimum temperature on grass for 1 week before sampling and the percentage infection of that sample gave a correlation coefficient of 0·66, a highly significant figure (0·3809 was required). The average minimum temperature on grass for 1 month before sampling gave an even more significant correlation, 0·7321. The highest correlation coefficient was 0·7528, which was obtained from the correlation of the percentage infection with the average temperature on the screen for one month before sampling. These figures are of undoubted interest but their true significance is difficult to judge in the absence of laboratory experiments under controlled conditions of humidity and temperature. A significant correlation can usually be obtained

Table 6

		Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Average number of thrips per sample on all plots, 1934–5		30·8	24·0	47·8	36·8	25·4	54·1	32·3	23·6	58·4	77·7	82·2	46·5	50·6
Percentage infection on each plot for 1933	14 U	—	1·7	7·2	10·1	4·3	8·6	—	40·0	16·5	—	—	—	—
	14 L	—	5·7	6·3	5·7	7·3	7·7	—	17·0	6·3	—	—	—	—
	13 U	—	1·0	1·2	3·2	3·9	11·9	—	17·0	2·0	—	—	—	—
	13 L	—	0·9	1·2	1·9	0·8	5·0	—	17·5	7·0	—	—	—	—
	(11[1] U)	—	—	—	—	—	—	—	—	—	—	—	—	—
	9 U	—	0·0	0·6	0·5	0·0	0·5	—	0·0	1·0	—	—	—	—
	9 L	—	0·9	8·6	6·7	4·7	18·1	—	29·4	17·9	—	—	—	—
	7 U	—	1·5	1·3	6·0	7·7	13·8	—	10·3	7·0	—	—	—	—
	7 L	—	4·9	7·9	9·1	2·9	23·4	—	7·9	3·0	—	—	—	—
	3 U	—	3·0	11·6	11·6	21·6	40·0	—	17·7	11·5	—	—	—	—
	3 L	—	5·8	8·3	11·2	9·9	31·7	—	13·0	3·0	—	—	—	—
Percentage infection on each plot for 1934–5	14 U	0·0	8·4	12·0	9·0	7·5	17·7	42·0	55·0	33·7	20·0	14·0	32·0	26·0
	14 L	0·0	7·5	6·0	4·7	5·6	12·6	21·0	34·7	14·7	14·0	6·0	16·0	8·0
	13 U	0·0	5·0	3·0	9·0	10·0	24·0	64·0	38·7	13·3	12·0	4·0	4·0	4·0
	13 L	0·0	7·1	1·0	2·1	4·0	20·8	30·9	23·6	9·3	8·9	4·0	4·0	12·0
	11[1] U	0·0	0·0	0·0	0·0	2·0	0·7	1·1	0·0	0·0	0·0	0·0	0·0	2·0
	9 U	0·0	0·0	0·0	2·0	0·0	0·7	4·4	1·0	0·0	2·0	0·0	0·0	2·0
	9 L	2·5	4·0	11·0	12·0	10·0	14·7	35·6	31·3	6·3	12·0	20·0	0·0	4·0
	7 U	4·0	4·9	3·7	7·6	9·1	3·2	8·7	5·3	2·7	6·0	0·0	0·0	4·0
	7 L	8·0	1·3	2·4	7·0	0·0	8·0	21·7	12·3	9·3	4·0	0·0	4·0	6·0
	3 U	0·0	6·0	12·7	13·0	14·0	12·0	22·2	11·5	4·0	0·0	10·0	4·0	8·0
	3 L	3·3	0·0	9·6	4·0	4·0	11·1	22·8	6·5	4·3	6·0	2·0	8·0	2·0
Percentage infection on all plots monthly for 1933	—	—	2·2	4·8	6·9	6·1	10·9	—	17·9	7·4	—	—	—	—
Percentage infection on all plots monthly for 1934–5	—	1·3	4·0	5·2	6·4	5·9	11·6	26·2	21·9	8·9	7·5	5·6	6·9	7·1
Average monthly temp. in ° F. (min. on grass) for 1933	—	—	30·3	33·9	41·0	44·0	50·9	48·6	46·5	39·8	—	—	—	—
Monthly sums of rainfall in mm. (8 in. gauge) for 1933	—	—	2·19	0·73	0·92	0·08	1·10	0·46	1·92	1·09	—	—	—	—
Average monthly temp. in ° F. (min. on grass) for 1934–5	—	26·8	28·5	34·8	38·3	44·8	47·2	45·3	43·9	39·6	34·7	36·7	31·7	32·5
Monthly sums of rainfall in mm. (8 in. gauge) for 1934–5	—	11·48	59·40	47·2	21·25	42·25	27·05	44·95	67·25	47·65	44·45	122·4	21·05	67·3

between temperature and the population of most animals that breed in the summer. Rise of temperature is only one of a number of complex factors that together constitute the change of environment at this season.

(2) *Effect of rainfall*

That rainfall might affect the nematode attack was considered possible but the correlation between infection and total rainfall for a month before sampling was negative and not significant. It would seem that dew provides sufficient moisture for the nematodes to complete the free-living stages of their life cycle.

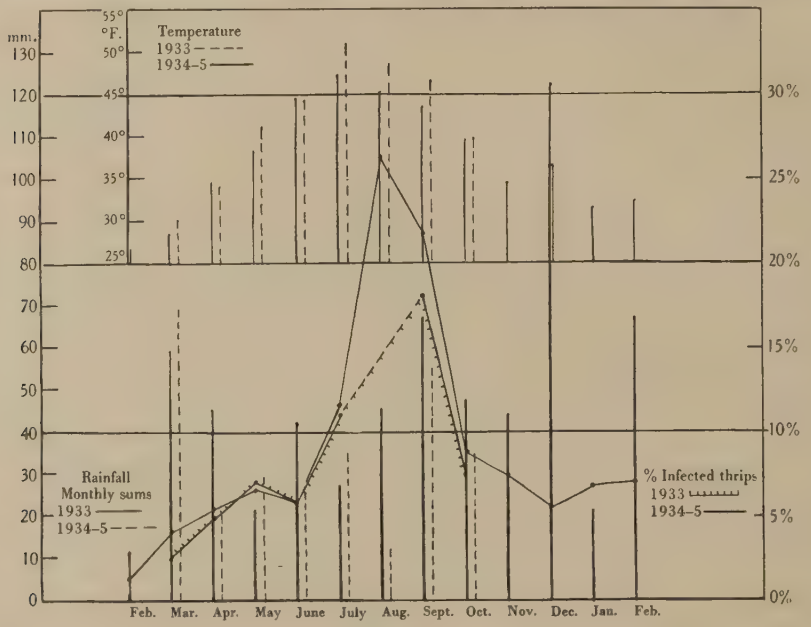


Fig. 3.

Heavy rain would most likely tend to wash them off the grass into the soil. Rainfall in relation to infection is shown in Figs. 3 and 5 and Table 7.

(3) *Total numbers of parasite and host*

A final point of some interest in the question of infection is raised by the population figures for both host and parasite plotted in Fig. 4 and Table 7. The abundance of the different stages of the nematode was estimated by multiplying together the average number of thrips in the weekly samples, the percentage of infected thrips and the average numbers of larvae or eggs found in an infected thrips. Presumably this would give a fairly accurate figure for the nematodes present on the volumes of grass in each sample.[1] The curve

[1] 4-lb. jars, capacity 2400 c.c.

expressing numbers of nematode larvae in a certain volume of grass attains its maximum in mid-July. At the same time the second brood of thrips reaches its peak (see Section 3 *a* and *b*). The average minimum temperature on grass is higher in July than at any other time. The percentage of thrips infected does not reach its maximum till 6 weeks later when the larvae of the second brood of thrips have attained maturity.

Table 7

Date 1934	Average population of thrips per sample 1934–5	Percentage of infected thrips	Calculated numbers of nematodes per sample		Rainfall before sampling (in mm.)	
			Larvae	Eggs	28 days	14 days
26 Feb.	31	1	2·48	3·16	6·48	2·60
5 Mar.	23	3	0·00	5·93	12·99	8·50
19	28	2	0·56	0·45	55·35	42·65
26	29	5	8·70	5·37	66·50	38·35
31	16	7	0·00	2·88	57·40	13·55
9 Apr.	28	2	1·12	3·25	42·25	3·90
16	37	4	0·00	24·72	22·35	7·80
26	61	8	0·00	48·84	30·40	24·65
30	64	6	7·68	109·82	47·20	39·40
7 May	50	7	15·00	148·40	57·60	44·70
14	44	5	63·80	111·10	55·10	15·70
22	26	6	71·76	40·87	46·05	6·05
28	27	7	103·95	47·44	21·25	5·55
4 June	16	4	37·12	9·86	6·95	0·90
28	35	7	68·60	74·48	35·45	29·00
4 July	35	5	66·50	71·75	42·15	34·50
9	57	10	397·10	181·26	38·50	27·15
17	72	12	440·64	247·10	44·65	14·30
23	54	16	423·36	298·94	52·95	31·00
30	52	16	399·36	231·30	29·75	20·65
6 Aug.	34	23	344·08	211·92	32·45	9·35
13	36	25	324·00	229·50	36·25	15·60
20	31	26	314·34	236·16	21·15	11·80
27	27	31	309·69	203·39	20·95	5·35
4 Sept.	25	19	209·00	136·80	58·05	48·65
10	27	22	237·60	163·35	52·45	47·10
17	23	21	*	*	75·90	27·25
25	19	20	197·60	83·98	62·05	39·70
1 Oct.	30	*	*	*	21·45	19·10
10	74	5	111·00	31·82	—	—
16	52	11	177·32	69·21	—	—
23	77	11	211·75	51·67	—	—
7 Nov.	80	8	179·20	30·08	—	—
22	76	7	74·48	37·77	—	—
12 Dec.	80	5	72·00	22·80	—	—
31	84	6	25·20	8·06	—	—
1935						
18 Jan.	46	7	12·88	17·71	—	—
11 Feb.	68	6	12·24	3·26	—	—
28	33	7	4·62	13·17	—	—

* No dissections.

The various generations of thrips overlap as the adults appear to live for some time. Taking Fig. 2 in conjunction with Fig. 4 it would appear that the high temperature in July greatly accelerates the rate of development of the nematodes and appears to increase their chance of survival in the free-living

stage. The numbers of infected thrips therefore show a steady increase after the July maximum although the number of eggs and larvae produced by the female nematodes undergoes a comparatively steady decline. The ideas suggested by the data expressed in these graphs are put forward with some diffidence as so many factors are involved.

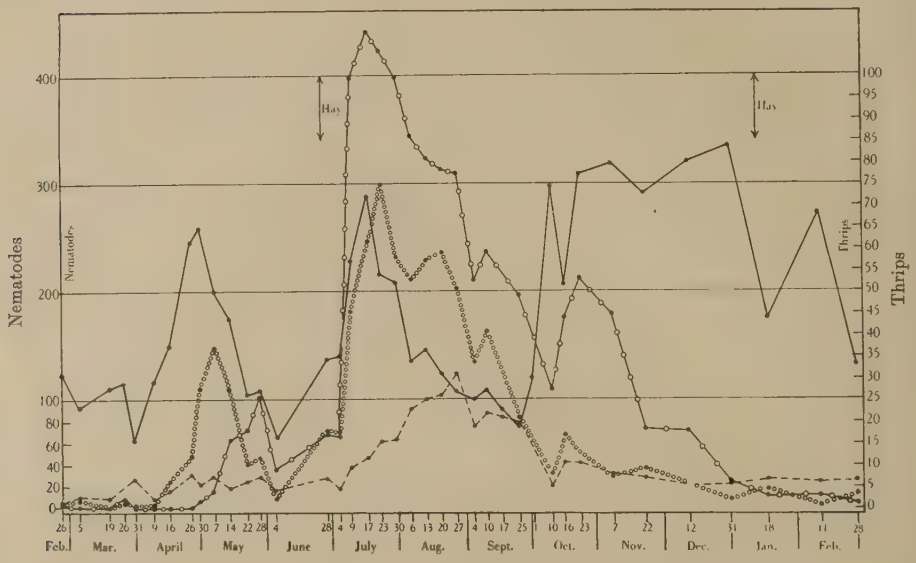


Fig. 4. Abundance of thrips and nematodes on all plots, 1934–5. Thrips (10-min. catches) ———, infected thrips (%) — — —. Nematode eggs ooooooooooo, nematode larvae —o—o—.

(*d*) *Morphological effect of parasite on host*

The effect of parasitism on the host is that sterility almost always follows. Amongst all the infected thrips dissected only 8 were found in which the reproductive organs appeared to be normal (Table 8).

Table 8

Date	Nematodes per thrips: Males	Females	Eggs	Larvae	Eggs of thrips
21. iii. 33	—	—	22	12	1
21. iii. 33	(1)	2	17	6	2
26. vi. 33	—	—	4	—	1
23. vii. 33	—	1	9	—	Ovaries well developed, no mature eggs
20. vi. 33	—	1	7	—	Mature eggs
17. vii. 34	(8)	—	—	18	1
31. iii. 34	—	1	—	—	1
13. viii. 34	—	—	—	2	1

It would be conceivable that, if the pupal host were parasitized at a late stage in its development, the eggs and ovaries would not at first be affected by the presence of the parasites. Sterility follows as a rule when only one immature parasitic female is present, but in three of the above cases the infection is fairly heavy. These three thrips were perhaps attacked in the late pupal stage. Very little is known about the exact effects of parasitism in insects.

3. VARIATION IN NUMBERS OF HOST INSECT

(*a*) *Evidence*

An estimate of the thrips population on all the plots was attempted in 1934. In 1933 I had noticed that they varied in number very considerably but I had no standard method to measure their abundance. The method used in

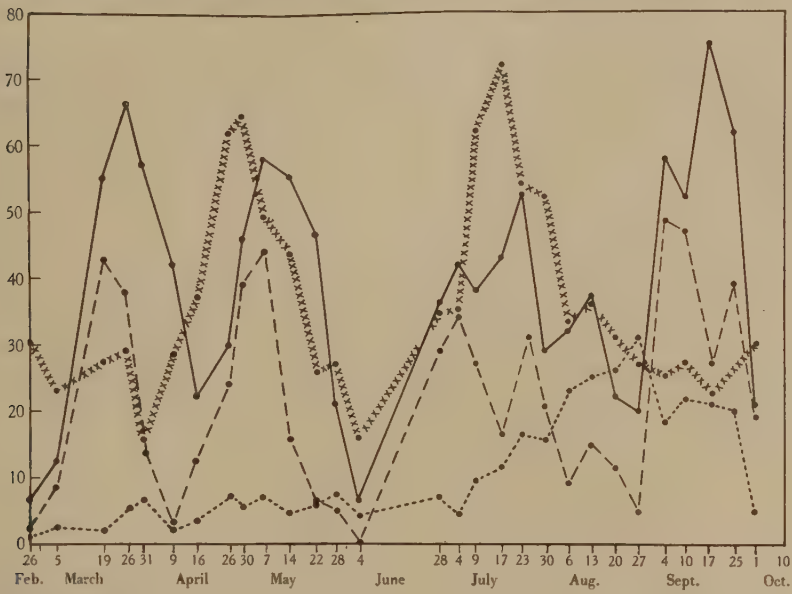


Fig. 5. Average numbers of thrips per sample xxxxxxxx; percentage nematode infection --------; total rainfall in mm. 28 days before sampling ————; total rainfall in mm. 14 days before sampling — — —.

1934 was to collect as many thrips as possible in 10 min. from samples of grass of about the same volume (2400 c.c.). This method was used because the amount of herbage on the manured and unmanured plots varied so much that it was impossible to take the grass from a given area. On a piece of ground 5 ft. square on 9 U in the late summer thousands of thrips would have been present and only a few score on the same area on 3 U and 3 L. On the whole

the thrips were much more abundant on some plots than on others but seasonal increases in the population on all of them were very similar.

Table 9

1934	Plot 3 U	Plot 3 L	Plot 7 U	Plot 7 L	Plot 9 U	Plot 9 L	Plot 11¹ U	Plot 13 U	Plot 13 L	Plot 14 U	Plot 14 L
26 Feb.	9	14	21	17	33	33	40	60	50	33	26
5 Mar.	6	14	18	12	28	31	9	45	26	24	41
19	8	16	10	14	42	26	31	54	50	32	23
26	4	8	20	15	54	21	46	52	32	40	30
31	4	4	8	5	25	14	45	18	20	15	16
9 Apr.	7	5	11	17	50	26	52	54	33	29	29
16	3	12	14	11	53	47	66	72	35	52	42
26	7	6	18	28	59	102	71	107	108	70	100
30	17	10	39	28	60	102	75	102	81	97	96
7 May	26	24	31	31	86	72	27	80	67	37	68
14	22	21	21	21	42	66	53	63	35	21	64
22	22	35	17	22	57	26	37	27	19	12	14
28	23	15	15	24	30	55	43	35	22	23	15
4 June	13	20	6	18	21	32	16	16	18	9	9
28	18	23	18	37	56	46	34	36	38	21	53
4 July	3	18	9	21	64	63	85	28	42	22	33
9	8	5	14	35	78	59	183	52	82	78	34
17	11	8	19	36	146	82	236	64	36	98	56
23	23	9	17	9	104	58	165	65	27	19	99
30	7	10	8	8	130	33	125	50	30	98	55
6 Aug.	17	6	8	18	58	25	76	42	22	32	68
13	5	7	9	18	86	36	35	32	13	94	66
20	17	9	2	20	58	25	60	22	8	72	52
27	25	7	9	11	56	17	38	37	10	38	53
4 Sept.	11	5	8	5	58	12	58	11	19	46	46
10	6	4	4	15	68	14	66	30	9	51	35
17	14	4	12	10	68	5	56	17	8	39	16
25	18	11	5	13	27	21	41	21	11	24	16
1 Oct.	12	16	21	24	81	32	63	27	9	31	17
10	26	22	21	38	223	128	126	88	62	51	34
16	40	19	18	34	127	45	58	68	47	83	30
23	31	72	16	46	192	105	106	66	45	110	61
7 Nov.	42	58	25	57	163	111	109	77	62	96	78
22	49	41	35	24	119	103	128	85	44	130	72
12 Dec.	45	57	47	105	150	82	120	78	65	62	74
31	73	79	54	81	98	108	42	98	40	112	137
18 Jan. 1935	9	25	24	23	110	52	97	63	56	37	14
11 Feb.	38	24	32	46	148	73	106	68	40	90	84
28	13	12	34	21	44	47	77	16	26	11	34
	730	755	718	1018	3152	2035	2901	2026	1447	2039	1890

Numbers of thrips found in 10-min. counts in laboratory samples.

The figures for individual plots from 26 February 1934 to 28 February 1935 are given in Table 9 and the monthly and weekly averages compiled from these are shown in Table 7 and Figs. 4, 5 and 6. More thrips occurred on 9 U and 11¹ U than on any other plots, 3152 on 9 U and 2901 on 11¹ U. These figures were significantly higher than the rest which varied between 718 on 7 U and 2039 on 14 U.

(*b*) *Effect of parasitism*

I do not think it probable that the absence of parasites on 9 U and 11¹ U is responsible for the higher population figures on these areas. Knechtel (1923) reports that *Aptinothrips rufus* was present in great numbers on the ears of *Holcus lanatus* in Roumania. It appears to be a favourite food plant and its

tufts provide plenty of shelter. *Aptinothrips rufus* seems to prefer a certain amount of shelter and has been found to be less abundant on the tops of the grasses.

Fig. 4 shows that the number of thrips which begins to decrease in late July reaches its lowest point on 25 September. The peak of infection by the nematodes was reached in August. At first sight therefore it would appear that parasitism might be affecting the population. This is improbable for two reasons. First, 9 U and 11[1] U both show a considerable drop in their population

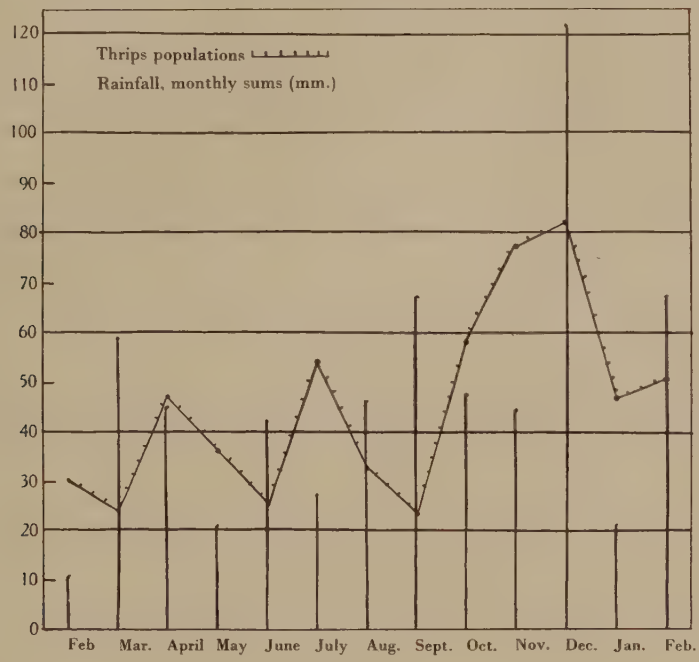


Fig. 6

figures for September. Secondly, the thrips show three peaks, one in April, a second in July and a third in the winter, extending from October to January. These three peaks are separated by deep depressions which are of fairly uniform depth, that in September being slightly shallower than the other two and these can have no connexion with nematode attack. It is therefore highly probable that the consistently higher population on 9 U and 11[1] U is due to the fact that *Aptinothrips rufus* prefers *Holcus lanatus* to the other grasses.

Aptinothrips rufus was bred on various grasses for experimental purposes but little difference was apparent in either the numbers or the vigour of the F_1 generation.

4. Difference in percentage parasitism on eleven plots

(*a*) *Evidence*

The present investigation was undertaken primarily to ascertain whether the apparent absence of the nematode on some plots was real and permanent. In 1933 the evidence proved that there was a significant difference in infesta-

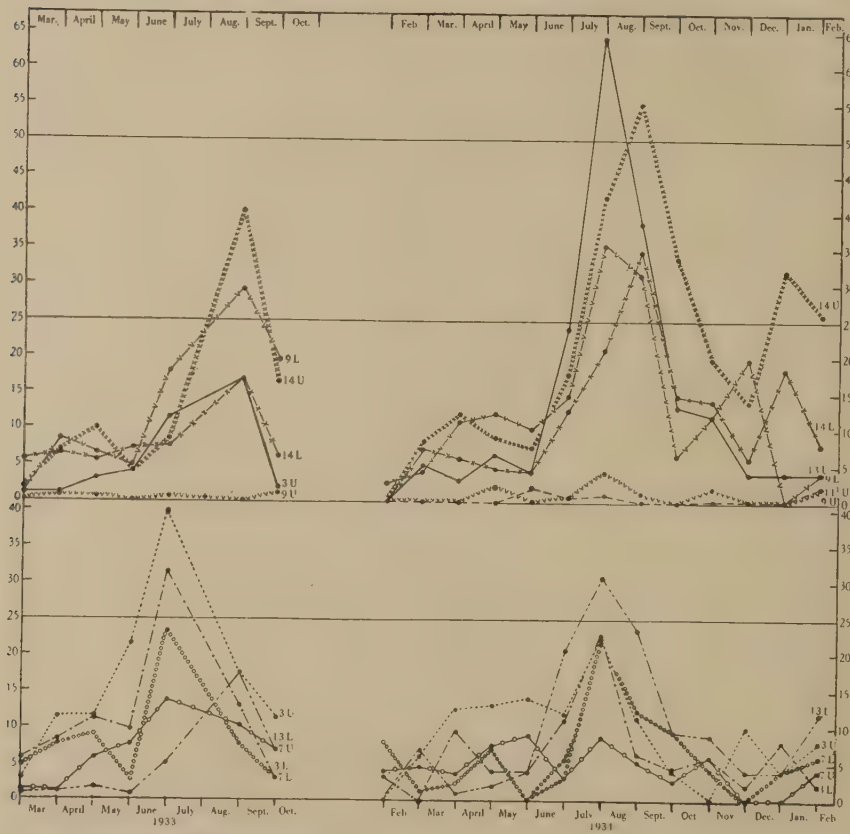


Fig. 7. Monthly percentage infection of thrips by nematodes. Plots 3 U ·····; 3 L —·—·—; 7 U —o—o—; 7 L ooooooooooo; 9 U vvvvvvvvv; 9 L —v—v—; 11^1 U – – – – –; 13 U ——; 13 L ——··——; 14 U xxxxxxxxxx; 14 L —x—x—x—

tion between 9 U and the other plots. In 1934 11^1 U was also sampled. Its vegetation is similar and its *p*H slightly lower. The percentage of thrips infested by nematodes is rather less than on 9 U.

Fig. 7 and Table 6 show the monthly average of infection on all the plots from 1933 to 1935. The highest infection on 9 U for any one month was 4 %

in August 1934, while in 1933 it failed to rise above 1 %. On 11^1 U it rose to 1 % in June 1934 and February 1935. In only 4 of 13 months was any infection found on this plot.

On each of the other nine plots infection rose to a marked degree during the summer months. On 13 U a heavy infestation occurred rising to 68 % in August 1934. On 7 U it was much lower, the highest point for 1934 being 8·5 % and for 1933 14 %. However if the curve for this plot be compared with those for 11^1 U and 9 U it will be seen to be consistently higher.

On comparing the infestation of any plot in 1933 with that in 1934 it is seen (Fig. 7, Table 10) that there is much variation and that infestation may be high in one season and low in another. In July 1933 infection on 3 U rose to 40 % but in 1934 only to 22 %. The curve for 3 L was somewhat similar though in 1933 it did not reach as high a maximum as 3 U. 7 L showed almost identical curves for both years but the maximum was reached a month later in 1934. 9 L also shows similar curves for both seasons. In 1933 infection on 13 U failed to rise above 17 %, but in 1934–5 it was higher than on any other and reached a monthly average of 64 % in August. This figure was taken from four weekly samples each over 60 %. The 1933 peak infection was thus quadrupled in 1934. 13 L with a maximum of 17·5 % in 1933 almost doubled this number in 1934, and 14 L shows a similar variation. 14 U on the other hand had a fairly high infection in 1933, a 40 % average in September; in 1934 a maximum of 55 % was reached in September, but, unlike the other plots, infection remained high throughout the winter months and reached an average of 32 % in January and 25·5 % in February, 1935. In February 1934 no infection was found on either 14 U or 14 L.

Table 10

	1933		1934	
Plot	Maximum % infection	Month	Maximum % infection	Month
3 U	40·0	July	22·2	Aug.
3 L	31·7	July	22·7	Aug.
7 U	13·8	July	8·7	Aug.
7 L	23·4	July	21·7	Aug.
9 U	1·0	Oct.	4·0	Aug.
9 L	29·4	Sept.	35·6	Aug.
11^1 U	—	—	2·0	June
13 U	17·0	Sept.	64·0	Aug.
13 L	17·5	Sept.	30·8	Aug.
14 U	40·0	Sept.	55·0	Sept.
14 L	17·0	Sept.	34·7	Sept.

From these observations it is obvious that the curve of infection fluctuates considerably throughout the seasons on all plots but that the range is much less on 9 U and 11^1 U.

(*b*) *Chemical factors*

The *p*H values (Table 1) for 9 U and 11¹ U are lower than for any other plot, but, on the other hand, the calculated correlation between *p*H values and infection over all the plots was not significant. In 1933 the correlation coefficient was 0·325 and 0·632 was required for this set of figures; in 1934 it was 0·332 while 0·632 was needed.

There has been a tendency in recent years to regard the *p*H of a soil as the most significant factor present. It must be remembered that *p*H is only one of a number of very highly complex factors influencing soil populations. Arrhenius (1921), working with soil samples with a *p*H value varying from 3-10, found that the earthworm *Perichaeta indica* Horst was able to survive only in soil with a *p*H of 6 or 7. As a result, perhaps, of his work there seems to have been a general belief that *p*H was important as a factor in controlling nematodes (Emmert, 1931). Vague references to such a theory occur quite frequently. Smith (1929), working on the relationship between physico-chemical properties of soil and abundance of *Heterodera* cysts, experimented with 78 soil samples and concluded that in the case of sandy soils there was no correlation. In peaty soils however he found a significant negative correlation between *p*H and cyst counts. Godfrey & Hagan (1933), working on soils with a *p*H varying from 3·5 to 8·5, found no correlation between *p*H and infection by *H. radicicola*, and Chandler's (1925) hookworm larvae were able to survive immersion in *N*/10 solutions (*p*H 1) of HCl for 18 hours when the temperature did not rise above 75° F.

I worked out correlations in order to estimate whether any significant relationship existed between the presence of *Anguillulina aptini* and the percentage of nitrogen in the herbage, weight of nitrogen per acre in the hay, percentage nitrification and the average mineralizable nitrogen but none of these was significant.

(*c*) *Botanical factors*

(1) *Experiments*

The growth of grass on the different plots varies according to the manurial treatments. Thus, in the plots under discussion, 11¹ U, 9 L and 9 U, 13 L and 13 U, 14 L and 14 U produce the heaviest crops of hay while the herbage on 7 U and 7 L is not nearly so rank. Both 3 U and 3 L produce very little grass and the thrips are much less abundant on these two as a rule. The lists of grasses given in Table 2 show that they are very mixed on most of the plots. *Arrhenatherum avenaceum* is very abundant on 14 U, *Alopecurus pratensis* on 13 L, but the only plots where one species is dominant are 9 U and 11¹ U. In 11¹ U *Holcus lanatus* has taken complete possession while on 9 U this species is dominant but a little *Anthoxanthum odoratum* is to be found.

It is known (Triffitt, 1934) that the secretions of some grasses influence the development of the eggs of *Heterodera schachtii* and I thought it possible that

Holcus lanatus might either harm the nematode by its secretions or hinder it from finding a host by its long and numerous hairs. To test this, two 6-in. cubes of turf were taken from each of the plots 9 U and 9 L and were placed in earthenware pots in the greenhouse. After fumigation with hydrocyanic gas they were examined and no living thrips could be found. On 1 May 50 thrips were placed on each lot of grass. The pots were treated as follows: 9 U A and 9 L A were both used as controls and 50 thrips from the original plots were placed on each. On 9 U B were placed 50 thrips from 9 L and on 9 L B 50 thrips from 9 U.

On 3 August the grass was cut and 25 thrips were taken from each of the four plots. Only 2 of these were infected by nematodes, 1 in 9 L A and 1 in 9 U B. In this one case, at any rate, it seemed possible for a nematode to complete its life cycle on *Holcus lanatus*. Such a small infestation was unsatisfactory, and at the beginning of September more thrips were taken from the plots and put on the grass. On 22 October 30 were taken from each pot and examined. The results are tabulated in Table 11. On neither pot infested with thrips from 9 U was there any infection. On the control pot 9 L A 23 % of the thrips were infected and on 9 U B (infected from 9 L) 20 %. It might be argued that the original thrips had survived and that no infection of the next generation had taken place but in that event one would expect to find a heavy infection in each insect whereas in only 3 out of the 13 were larval nematodes abundant and males present; the majority contained females and eggs with very few larvae.

These results are strong evidence against the theory that any secretion from *H. lanatus* inhibited the development of the nematode.

Table 11

Experiment	No. thrips ex.	No. thrips inf.		Nematodes: Males	Females	Eggs	Larvae
9 U A (control)	30	0		—	—	—	—
9 U B	30	6	(1)	—	2	—	—
			(2)	—	1	9	14
			(3)	—	1	—	—
			(4)	—	4	—	—
			(5)	—	1	6	2
			(6)	—	2	—	5
9 L A (control)	30	7	(1)	—	4	—	—
			(2)	1	1	13	62
			(3)	1	1	14	26
			(4)	—	4	—	—
			(5)	—	3	2	—
			(6)	1	2	—	26
			(7)	—	4	—	15
9 L B	30	0					

The *p*H values of the soils were taken at the end of the experiments and are as follows, 9 U A 3·65, 9 U B 3·95, 9 L A 5·15, 9 L B 6·4. These gave additional proof that a low *p*H was not a directly important factor in preventing the nematodes from completing their development.

(2) *Discussion*

It appears that some conditions were present in the greenhouse experiments which were not found on the plots, and the two most obvious of these are the rankness of *Holcus lanatus* on 9 U as opposed to the more delicate growth under greenhouse conditions, and secondly the high humidity which exists in the cellophane cages in the greenhouse.

H. lanatus in midsummer on 9 U is extremely coarse and the sheaths of its stems are of great length. Short lengths of stems have been kept in the laboratory in Petri dishes and thrips of varying age have been placed on them. Almost invariably the insects sheltered in the curling edges of the blades and seemed unable to penetrate into the sheath for more than a few mm., if at all. In the field it is probable that the larvae and pupae do not penetrate into the sheath at all but shelter at the base of the blade just where it leaves the sheath. The nematode is much smaller than the host and it may make its way down into the sheath for a considerable distance. If that is so it may have difficulty, when it has matured, in finding the host. There are so many more species of grasses on the other plots that even if some, such *Dactylis glomerata*, have long rank sheaths there are still numerous finer and smaller grasses where these conditions would not be present. In *H. lanatus* the hairs on the leaf hold rain in large drops and prevent its running down into the sheaths; the sheaths of more open grasses with less velvety leaves are likely to have a higher humidity.

In the greenhouse experiments growth was never as vigorous as it is under external conditions and the grass was cut on several occasions. Also in the cellophane cages humidity is exceptionally high. Actual measurements have not been carried out; but dew remains on the grass till much later in the day than it does on the grasses just outside the greenhouse. The nematode which was seeking a host in any of the greenhouse cages would have a short distance to travel on account of the small size of the grass, while the excessive humidity would be an added advantage and give it a longer period to seek the host without danger of desiccation.

At present it is not known for how long the female nematode can survive without finding the host. Development may occur within a short time of fertilization, or alternatively it may be delayed till some kind of stimulation is set up by the blood of the host. It would appear that there is a definite critical period at this stage.

It should be noted that the possibility of the absence of infection on 9 U and 11[1] U being due merely to geographical position was raised, but as infected thrips occur round the edges of 9 U this does not appear to be a likely factor. Spreading from one plot to another must occur by means of wind and mechanical agents, but this cannot take place to any extent in view of the definite differences between adjacent plots.

(d) Parasites other than the nematode

Unidentified *Trombidium* larvae have been found firmly attached to the hind coxa of a number of specimens of *Aptinothrips rufus* during the late spring. Ten were found in May and one in mid-July. In no instance did they appear to have exerted any malign influence on the host. The ovaries appeared normal and the insects healthy and active.

Spores of an unidentified fungus were found in the body cavity of *A. rufus*. Thirty-four insects were found to be infected: sterility seems to result.

5. Discussion

The observations made on the thrips population over a short period indicate that parasitism by the nematodes does not appear to exert a profound influence on the abundance of the insects.

The effect of the parasite on individual insects suggests that the next step in the investigation should be the culturing of the nematodes in hanging drops. This presents numerous difficulties which, however, should not be insurmountable. If the free-living female nematodes could be obtained thus it should be possible to infect larval and pupal thrips and so gain information about the causes of sterility. This may be due to a toxin or it may be due to the absorption of protein by the nematode. According to Norris (1933, 1934) most adult insects need protein for the normal development of their genital products.

Biological control extends over such a large field that, although *Aptinothrips rufus* is not itself of economic importance, much fundamental information might be gained by continuing the investigation along these lines.

6. Summary

1. *Aptinothrips rufus* Gmelin is abundant on the grass plots of the classical field Park Grass at Rothamsted Experimental Station. Sampling has been carried out for 2 years on a number of the plots and population counts have been made.

2. *A. rufus* is parasitized by *Anguillulina aptini* (Sharga). Some experimental work on the biology of the nematode has been carried out.

3. The nematode is rarely found on two of the plots and this difference in distribution was found to be constant during 1933 and 1934. There is a very rank growth of *Holcus lanatus* on these two plots and the coarseness of this growth appears to exert an unfavourable effect on the nematodes. Infected insects have been bred on a less sturdy growth of *H. lanatus* under greenhouse conditions.

4. An account is given of other factors which might affect the distribution of the nematode.

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TERRITORY IN THE YELLOW FIELD ANT, *ACANTHOMYOPS FLAVUS*

By E. CAREY and C. DIVER

In a recent paper Pickles (**1**) states that he has never seen workers of *Acanthomyops flavus* F. travelling outside the nest mound, and he assumes that it can safely be said that the species has no "territory" in which it forages for food.

These ants are mainly, if not exclusively, subterranean in habit, hence it is difficult to determine the extent of their movement away from the nest; but recent observations of ours leave little doubt that foraging outside the area of the nest does in fact take place. In view of this and of the fact that our observations indicate a method of mapping, at least approximately, the territory occupied, it seemed advisable to publish the results of our inquiry as far as they have gone.

This species is stated (**2**) to cultivate root Aphids (though we were not aware of this at the time of our observations), and thus, if there is no foraging, the ants must depend upon the Aphid population already existing in the site chosen for the nest.

During preliminary work on a survey of the ant population of South Haven Peninsula, Dorset, a few selected areas presenting contrasting type of habitat were examined in 1935. One of these was Redhorn Quay, a turf promontory, with an area of about 900 sq. yd. or one-fifth of an acre, projecting westwards into Poole Harbour and surrounded by a gravel beach. This quay was constructed early in the nineteenth century and at present consists of between 1 and 2 in. of earth covering a bed of solid clay. The plant carpet is short mixed turf containing some 50 species among which are scattered clumps of taller plants such as dock (*Rumex crispus* L.), ragwort (*Senecio jacobaea* L.), and thistles (*Carduus tenuiflorus* Curt, and *Cnicus lanceolatus* Willd.).

The area was mapped in detail and the sites of these clumps determined. There were no obvious *Acanthomyops* mounds so, in order to test for the presence of these species, a series of random digs with a fern trowel was made. The first tests showed that yellow *Acanthomyops* tended to concentrate round the roots of certain plants, and this clue was followed up by lifting all the docks, most of the ragwort and large random samples of the principal thistle clumps. As a check on this three open turf areas were examined by a series of digs at given intervals. Both *A. flavus* and *A. umbratus* were present and seemed to be behaving in a similar manner, but so far a sufficient number of specimens has not been identified to enable the distributions of the two species to be dealt with separately. Taking both species together the results are shown in the following table.

Type of dig	% of digs in which present	Total no. of digs	Value of P*
Cnicus lanceolatus	75	24	0·0000
Rumex crispus	64	36	0·0000
Carduus tenuiflorus	26	65	0·005
Senecio jacobaea	21	14	0·07
Open turf	6	79	—

* The value of P given here is that derived from comparing the samples of the particular species with the open turf samples by means of the χ^2 test.

The figures show either that the ants have a definite predilection for visiting the roots of certain species, or that the distribution of these species and of the ants are indirectly associated through some soil or other factor undetermined. We hope, later, to test these hypotheses by comparing the distribution of root Aphids. *Senecio jacobaea*, though ants were found round some of the plants, is not significantly more popular than ordinary turf; the same applies to *Carduus tenuiflorus* if one clump is excluded. This exceptional clump is a rough line including 12 *tenuiflorus* round 8 of which ants were found. If this clump is compared with the remaining clumps of this species, the probability of their being random samples of the same population is given by $P = 0{\cdot}0002$. The remaining *tenuiflorus* plants, which clump by clump show a uniformly low percentage of occupation, compared with the open turf give $P = 0{\cdot}1$. In this case as in *Senecio jacobaea* the evidence suggests that these plants are only visited if they happen to grow near a centre of ant population, the exceptional clump being reasonably close to plants of *Cnicus lanceolatus* and *Rumex*. *R. crispus* ($P = 0{\cdot}0002$) and *Cnicus lanceolatus* ($P = 0{\cdot}00003$) are significantly more popular than *C. tenuiflorus* even with the exceptional clump included. The popularity of the docks is more striking than the figures indicate for the only plants at which ants were not found were either growing in extremely hard gravelly ground or were very small rosettes. The reason for this popularity cannot be stated because the roots were not examined for Aphids; but since then Aphids have been found on the tap roots of other docks.

In only two cases was the presence of these ants at plant roots (as opposed to open turf) attributed to the presence of a nest at that spot; in general the ants were present in small numbers and there were no signs of chambers or pupae. Several nests were located, however, and these were in the open turf zones usually under stones; occasionally they were indicated by a very slight upraising of the ground, but there were no hummocks for which, it is suggested, the extreme shallowness of the soil may be responsible.

In view of these facts and of the siting of the known nests, there seems presumptive evidence for supposing that yellow *Acanthomyops* have a foraging territory, and that a ready method of determining this lies in the examination of the roots of certain species of plants.

We are much indebted to P. Lupton and J. Lester for help in the field.

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1. **Pickles, W. (1936).** "Populations and territories of the ants, *Formica fusca*, *Acanthomyops flavus*, and *Myrmica ruginodis*, at Thornhill (Yorks)." J. Anim. Ecol. 5: 262–70.
2. **Donisthorpe, H. St J. K. (1927).** "British ants." 2nd ed. London.

REVIEWS

THE FEBRUARY ISSUE OF *THE JOURNAL OF ECOLOGY* (Vol. 25, No. 1, 1937)

This issue contains nine original contributions, including two which deal with the distribution of species. The longest (nearly 100 pages) is Prof. Matthews' elaboration of his Presidential Address to the Society delivered in January 1935, on the "Geographical Relations of the British Flora". Prof. Matthews has reclassified British species of Flowering Plants according to their total world range, and recognizes eleven geographical "elements" excluding the species of universal, Northern Hemisphere, or general Eurasian or European distribution. This important paper is illustrated by a number of maps. Dr H. H. Allan shows that there are many difficulties in applying Raunkiaer's "biological spectra" to the flora of New Zealand, and criticizes the method from several points of view.

Mr E. W. Jones describes for the first time the vegetation of Grimsey, an island lying off the north of Iceland, and shows that it has many peculiarities, the causes of which he discusses. Mr P. L. Anand describes the algal vegetation of south English chalk cliffs in two localities—Birchington in Kent and Beachy Head in Sussex—and in each he recognizes four horizontal zones, all affected by the salt spray. Dr A. S. Watt continues his "Studies in the Ecology of Breckland" with a paper on the origin and development of "blow-outs". Dr B. N. Singh and Mr G. V. Chalam present a short but interesting quantitative analysis of numbers of individuals of different species in the weed flora of an area of arable land in India, comparing their results with those of others who have recently treated this subject statistically. Dr S. A. Waksman chemically analyses a "heather peat" profile from the Moorfoot Hills in Scotland, and finds that its composition shows more affinities with "low moor" than with "high moor" peat. This result, together with the fact that the peat was about eight times as thick as any British peat known to be formed by *Calluna* and its immediate associates, suggests that the heather was growing on peat formed by other plants. Mr G. Milne considers the soil relations of two well-marked types of East African vegetation. Messrs Marsden Jones and Turrill present their fourth report on the transplant experiments at Potterne.

Reviews deal with the *Journal of Animal Ecology*, books on the post-Glacial and historical development of Britain, British farming treated regionally, Welsh grasslands, the ecology of the tsetse flies, East African soils, etc.

There is also an account of the British Ecological Society's summer excursion in south-western Ireland and of the Annual Meeting in January at University College, London, together with a statement of accounts for 1936 (showing that income and expenditure just about balanced); also the current list of members of the Society.

A. G. TANSLEY.

A SOUTHERN COSMOS

(1) **E. R. Gunther (1936).** *A report on oceanographical investigations in the Peru coastal current.* Discovery Reports, 13: 107–276; 71 text-figures and 3 plates. Cambridge University Press. Price £1. 6*s*.

(2) **Robert Cushman Murphy (1936).** *Oceanic birds of South America.* 2 vols.; 1245 pp.; 80 text-figures, 16 coloured and 72 uncoloured plates. American Museum of Natural History, New York. Price $10.50.

(1) These two authors approach a single gigantic ecological phenomenon from opposite ends. Or rather they revolve round it, reviewing it from different aspects. The oceanographical cruise of R.R.S. "William Scoresby" in 1931 aimed at a description and analysis of the Peru

Coastal Current, which is a complex belt of cold water that appears near the west coast of South America as far north as the boundary of Peru and Ecuador. (It is no longer called Humboldt's Current, since this pleasanter name is not precise enough to suit the rigid requirements of oceanography. This seems a pity, since no honour to Humboldt from ecologists could be too high.)

The main gist of this report is that the cold water comes somehow north from Antarctic regions and swirls up to the surface in several areas; it is not therefore by any means a surface drift from the south. The variations in its appearance, and in the corresponding distribution of warmer water, are vital to many sea-birds and plankton animals. The warm current, "Aguaje", causes great changes in colour of the ocean, due partly to plankton mortality. Fish die, and with them also other animals. A squid mortality off Chile, of which a remarkable photograph is given, is attributed to periodic inshore migration from some other cause. The report is precise and impressive. A less technical account can be read in the *Geographical Journal*, 1936, 88: 37–65.

(2) This is a magnificently produced work, the culmination of a lifetime's industry. The pictures illustrate a fascinating world of oceanic bird life and the text is completely documented and full of valuable information, not only to the museum specialist, but to ecologists generally. The author to begin with surveys the vast theatre of his study: its geography and winds; history of exploration; the ocean currents and their types of life; the food of the birds; islands that afford nesting places—and produce the guano industry. Then each species is exhaustively reviewed. The most interesting ecological is the discussion of "El Nino", the devastating tropical counter-current that periodically kills the plankton on which various guano birds feed, and so causes widespread starvation and death among the birds themselves. El Nino is a current of hot, less saline water, part of the Equatorial counter-current. The organisms adapted to the cool, more saline Peru Coastal current cannot survive the change. Mortality is sometimes so great that H_2S is produced in quantities sufficient to blacken the paint on ships. The periodic development of El Nino is one of the most drastic ecological periodicities in the world and it takes place in a region full of other biological interest which Dr Murphy's book brings out to a superlative degree.

CHARLES ELTON.

PLANKTON DYNAMICS

A. C. Hardy & E. R. Gunther (1935). *The plankton of the South Georgia whaling grounds and adjacent waters*, 1926–27. Discovery Reports, 11: 1–456; with 193 text-figures. Cambridge University Press. Price £2. 10*s*.

When the results of about eight months' plankton hauling run to 456 pages, which measure $12\frac{1}{2} \times 9\frac{1}{2}$ in. and weigh several pounds, the ecological reader may well begin to wish that he had the voracity and single-minded interest of the fin whale itself, which lives exclusively on one kind of Crustacean, *Euphausia superba*, putting it away in enormous quantities. This report, however, has not simply a practical or local geographical interest, but forms a masterly survey of the whole framework of Antarctic plankton investigation, including water conditions, the phytoplankton, the zooplankton, and the relation of these to each other and to whale populations—and consequently to the whaling industry.

The report goes even deeper than this, setting out a theory of plankton behaviour, for which Hardy is mainly responsible, although he acknowledges carefully the early observations and ideas of other workers such as Castracane (1885) and Pearcey (1885).

This theory rests partly on some well-ascertained and rather unexpected facts of plankton distribution. The first is that plankton is very patchy in its occurrence, the patches being often a mile or two across, but often rather sharply bounded. This patchiness has been investigated by Hardy by means of his continuous plankton recorder (see Discovery Reports, 1936, 11: 457–510 & 511–38), and also by the ordinary means, with which the main report chiefly deals.

The second fact is an undoubted tendency for dense phytoplankton to be poor in animal life: the best known example is the avoidance of *Phaeocystis* shoals in the North Sea by migrating herring. There is in fact a somewhat inverse correlation between phyto- and zooplankton. The whale concentrations off South Georgia showed the same phenomenon very strikingly, since the whales were on one side and the dense phytoplankton on the other. The scarcity of phytoplankton is correlated with *high* and not *low* concentrations of nutrient salts.

Two theories hold the field. One is that overgrazing by zooplankton (chiefly Copepod and Euphausid Crustacea) causes temporary scarcity of phytoplankton. The other is that the animals *avoid* dense phytoplankton owing probably to chemical and physical conditions in such patches. Hardy favours a combination of the two processes: he adds a working hypothesis as to how "animal exclusion" might work. It is established that the phytoplankton stays in the upper layers: the zooplankton goes deep down in the day, coming up "to graze" at night. Since different water layers move in different directions at various speeds, there is possibly here a method of sorting out organisms, according to how long they stay up feeding. It is obviously impossible to retail the massive evidence that forms the background of this survey, or the detailed and ingenious arguments used in the hypothesis. The whole report is worthy of careful study, which could perhaps have been made less formidable a task if the editor had pruned some pages of the hypothetical reasoning. The lay-out and lucidity deserve high praise.

CHARLES ELTON.

SOIL COMMUNITIES IN CENTRAL EUROPE

Gerhard Frenzel (1936). *Untersuchungen über die Tierwelt des Wiesenbodens.* 130 pp. Gustav Fischer, Jena. Price RM. 4.50.

Dr Gerhard Frenzel, assistant in the Zoological Museum of Breslau University, following in the steps of Morris, Cameron, Buckle and other British workers, has made a very thorough comparative study of soil faunas in various parts of Silesia. Samples were taken during the period April 1933 to April 1934 from four meadows in the flat country near Breslau (height 110 m.), from three on the slopes of the Sudetes Mountains (670, 800 and 1200 m.) on the Czechoslovakian border; and also, during July 1933, from two areas in the Central Carpathians (1700 and 2000 m.). Details are given of dominant plants, simple soil analyses, *p*H and general characters of these areas, indicating wide differences in the physical environments of each type. It is concluded that soil moisture, depending on soil structure, is the most important of the factors influencing the population.

In sampling, after removal of the surface vegetation, soil was taken from a quadrat of 25×25 cm. at successive depths of 5 cm. down to 25 cm. Within this quadrat one of 10×10 cm. was used for counting the smaller organisms, while larger species (earthworms, beetle larvae, etc.) were counted from the whole large quadrat by hand picking. The small organisms were counted microscopically after extraction by means of a Berlese apparatus.

Before discussing his results Dr Frenzel makes an interesting division of the soil fauna into three types. Animals which normally pass through their whole existence, from egg to death, within the soil are called "*geobiont*". Those passing part of their life, generally the developmental stages, below ground are called "*geophil*", while the adjective "*geoxen*" is applied to those which are found regularly in the soil but are perhaps accidentals, being more properly associated with the vegetation layer above. "*Geobiont*" organisms include only the Lumbricidae, Geophilidae, *Scutigerella immaculata* and two nematodes; by far the greatest number of species belongs to the two latter classes. These distinctions are, I think, useful ones, though at times perhaps difficult to draw. Actually the soil animals and those normally living in the vegetation layer above must be regarded as forming separate communities which, during certain diurnal or seasonal changes in the environment, become more or less linked.

Altogether 422 species were identified and are tabulated with indications of presence or absence in the various habitats studied. The number of species in each habitat varies between

68 and 203, but it is noticeable that there is a positive correlation between the number of samples taken in each area and the number of species found. Numerical data, however, are only given for the relative proportions of orders throughout the year and at the times of sampling. More numerous samples, while they would have increased the numbers of species listed in some of the habitats, would probably not have altered appreciably the proportions of orders already obtained.

There is considerable correspondence between the Silesian and British soil faunas, many species listed for the former having occurred in soil surveys in this country. Attention is drawn to species showing marked ecological plasticity (*Leitformen*), which occur in all areas studied. These include 2 nematodes; 1 Gastropod; 7 Collembola (all common soil species in Britain); 22 mites and larvae of Elateridae; Itonididae (Cecidomyidae); Tendipediae (Chironomidae) and Dolichipodidae. This method of comparing the faunas of series of habitats is one which, undoubtedly, is going to be of great value to ecology, the idea of ecological plasticity having already been used with much success by Russian workers on the ecology of the Orthoptera.

In all areas together, mites form 42·4 % and Collembola 30·9 % of the population, in respect of numbers of individuals; but with regard to numbers of species, while mites are still in a majority, with 41·8 %, the Coleoptera come next with 19·8 %, Collembola forming only 7·8 %. These results are in general agreement with previous work in this country.

The importance of springtails and mites in the general economy of terrestrial communities is now well recognized; they form not only the "key-industry" upon which many carnivorous animals ultimately depend but also, by their saprophagous habits, must influence greatly the transformation of organic matter in the soil. Dr Frenzel has demonstrated that in comparatively dry localities mites predominate over springtails, while in damper areas the latter are most abundant, a fact to be expected in consideration of the morphology as well as of the humidity requirements of the two groups.

The soil faunal maximum is shown to occur in October, followed by another peak in early spring, with midwinter and midsummer minima. In view, however, of the rapidity with which Collembolan populations appear to fluctuate, it is doubtful if samples were taken frequently enough for the curves to be any more than rough approximations to the actual. Individual points on the curves are very probably representative of the state of the populations at the times at which they were taken (Thompson, 1924, *Ann. Appl. Biol.* 11: 349, demonstrated a remarkable uniformity in distribution of soil species): it is the direction of the curves between these points which must remain doubtful. It is in this that the work under discussion suffers and a hope may be expressed that with the recently devised apparatus for extraction of soil organisms, this fault, hitherto common to all soil surveys, may be remedied.

There is a large bibliography and the paper is well indexed. The list of species is probably the most comprehensive yet made for soil communities and the large sections devoted to discussions of the habits of various soil organisms provides a valuable summary of our knowledge of this subject.

JOHN FORD.

THE ECOLOGY OF SLEEPING SICKNESS

C. F. M. Swynnerton (1936). *The tsetse flies of East Africa. A first study of their ecology, with a view to their control.* Trans. R. Ent. Soc. Lond. 84: xxxvi+579 pp.; 33 figures, 22 plates, 7 maps. Price £5. 10*s*.

This volume is the review and summary of the work of the Tsetse Fly Research Department of Tanganyika Territory during the period 1931–4. While dealing essentially with the ecology and habits of tsetse flies, the width of scope of the investigation makes the work profitable reading for all interested in the ecology of the Tanganyika region. The volume opens with discussions of the problems of tsetse fly research, the areas affected, the extent of

infestation, and the methods of investigation. The author is at all times conscious of the importance of knowing the interrelationships of the flies to their biotic as well as physical environment, and this is well demonstrated in the sections dealing with the general ecology of the area; the distribution of the principal plant and animal communities, the plant communities and their respective physical factors, the relation of diurnal and nocturnal vertebrates to the flies, and their enemies—all with particular reference to the ecology of the flies, but conveying valuable information in concise form as to the general bio-ecology of the area. There are also included sections dealing with the vegetation types not habitable by the flies, summaries of laboratory results on physical factors and the developmental rates of the flies, experiments dealing with attack methods, the forming of fly barriers, and the methods of defence against attack. In the appendix are included representative data of the investigation, a key to the adults and pupae of East African species of tsetse flies, a consideration of game reserves in the area, and a list of the dominant plants and the predominant animals in connexion with a distribution map for plants, and one for animals. There is also a very useful 38 page summary of the entire work which should be very valuable for workers wishing to be informed on the general aspects of the problem, but unable to devote the time necessary to go through the necessarily deep details. Interaction has been afforded an important place and a detailed food-chain shows the biotic connexions and interrelationships of the flies. The study is an excellent example of large-scale field research financed by Government and carried out with the principles of community ecology as a working basis.

J. RICHARD CARPENTER.

THE BEHAVIOUR OF BIRDS OF PREY

Heinz Brüll (1937). *Das Leben deutscher Greifvögel: die Umwelt der Raubvögel unter besonderen Berücksichtigung des Habichts, Bussards und Wanderfalken.* 144 pp.; 47 text-figures and plates. Gustav Fischer, Jena. Price RM. 6.

The purpose of this paper is to understand bird behaviour, which is perfected in accordance with the development of the senses and other organs of adaptation, and so to represent the German birds of prey as organisms which actively construct their habitats from the material of their environments. It is thus meant to be a psychological explanation of observations made by the author in the field, as well as taken from his experience as a falconer in training birds. Much supporting evidence is drawn from recent physiological studies in Germany.

In accord with the theory of von Uexküll, the bird's environment is divided into four fields of activity: physical environment, sex, the enemy, and food. The physical environment and the enemy require permanent attention on the part of the bird; food and sex are periodic phenomena. In every field of activity there are various stimuli to which the bird reacts in definite ways. Brüll portrays the bird in each field, and enumerates and describes the stimulating factors and the reactions to these. Part of the paper is devoted to the problems of falconry, in which art or science the author is apparently well versed.

On the basis of this material, three natural groups of birds of prey are distinguished, the goshawk (*Accipiter gentilis*), buzzard (*Buteo buteo*) and falcon (*Falco peregrinus*) being cited as typical representatives. Their varying interests do not clash, for each group occupies a definite type of habitat to which it is perfectly adapted. Thus the goshawk, with its short, round wings and its long tail, is associated with woodland or cover, where it may be seen in its typical short, hunting flights. The buzzard, however, is adapted to both woodland and meadow; its long, broad wings prepare it for a characteristic hovering flight. Typical of the other extreme is the falcon, for it has long, narrow and pointed wings, and demands open country, exhibiting a swift and powerful flight.

The bird's relation to its habitat is further expressed by its nesting habits; it must be able to approach and to leave the nest without hindrance. Hence the falcon may select a flat place

on the cliffs, while the goshawk or buzzard will build in a tree-top. The plumage of the downy young presents a contrast in black and white, towards which the feeding activity of the adults is directed; as this plumage merges into that of the immature bird, the adult's activity changes and its ties with the nest are weakened.

Throughout its behaviour the bird makes use of many signs or marks. Movement, form and colour are all of importance in revealing its prey. When the bird is hungry, the red colour of blood is associated with food; but it is not significant when the bird is in another field of activity. Characteristic mating-flights, accompanied at times by calls and notes, serve to lure its mate; among the nocturnal birds of prey, the owls, a certain intensity of light seems to be the necessary stimulus to this behaviour. Practical use of this sort of knowledge is made by the falconer, whose gloved fist comes to represent divers factors in the various fields of the hawk's activities.

Brüll's theory seems to be that these birds act in relation to definite objects in their environments, which attain significance at certain periods and lose it at others. This emphasizes the physiological rather than the psychological, and the two are apparently confused throughout the paper. Though it is an interesting hypothesis, it requires the support of more extensive observation and experimental research. The illustrations are good, and the paper follows a carefully planned, systematic outline. The ecologist will welcome this approach to the study of bird behaviour, and if he will persevere in the face of a rather tedious style he will be rewarded with a wealth of interesting material.

FRANCIS EVANS.

GRASSHOPPERS AND CRICKETS

Malcolm Burr (1936). *British grasshoppers and their allies: a stimulus to their study.* 162 pp.; 6 plates, 56 drawings, and 40 maps. Philip Allan and Co., 69 Great Russell Street, London, W.C. 1. Price 6*s*.

THERE are 31 Orthoptera on the British list, not counting occasional immigrant locusts and the half dozen cockroaches and crickets that have been imported. Several of these species are very rare, and about half of them are so far recorded only from Southern, South-Central, and Eastern England. Yet they are striking and often abundant members of a wide range of animal communities: woods, scrub, meadows, dry pastures, sandy heaths, dunes, marshes, bogs and houses.

This small book ($7 \times 4\frac{1}{2}$ in.), with its brief general description of the groups and illustrated diagnosis of every species, backed in each case by a distribution map, will be extremely useful to ecologists. One of the author's aims is to attract the interest of field workers, since the distribution habits and life-histories are still very imperfectly known.

The 31 species comprise 3 wild cockroaches (*Ectobius*), 3 ground-hoppers or grouse-locusts (*Tettix* or *Tetrix*, now *Acrydium*), 11 grasshoppers (Acrididae), 1 mole cricket (*Gryllotalpa*), 3 true crickets (Gryllidae), and 11 bush crickets (Tettigoniidae). These insects are, however, only the impoverished fringe of a much richer Eurasian fauna of Orthoptera—there are 500–600 species in Europe alone. The book, therefore, gains enormously in value by its references to some nearby allied European species, which may turn out to live in this country. The author, who is a noted linguist, and had travelled much abroad, is well qualified to give an opinion on this aspect of the group.

The earwigs, which are not Orthoptera, are thrown in as a useful extra item: 5 native and several imported species.

As regards distribution maps: there is no means of checking them, since the author gives practically no references at all to literature. One map, at any rate, disagrees with the text: *Mecostethus grossus* "has been recorded from scattered localities, but not yet north of the Wash". The map, however, marks it in the county of Angus in east Scotland. The lack of references is also felt on the ecological side. We should at least expect mention of the full study by the Divers of grasshoppers habitats on Studland Heath (this *Journal*, 1932, 2: 36–69).

Otherwise, the book leaves an impression of careful workmanship and refreshing clarity. Ecologists need about fifty more books of the same kind, dealing with other invertebrate groups in the British Isles.

CHARLES ELTON.

AMERICAN GAME RESEARCH

(1) E. Lowell Sumner Jr. (1935). *A life history study of the California quail, with recommendations for conservation and management.* California Fish and Game, 21: 167–256 & 277–342. 58 text-figures and photographs.

(2) Paul L. Errington & F. N. Hamerstrom Jr. (1936). *The northern bob-white's winter territory.* Research Bull. Iowa Agric. Exp. Sta. 201: 305–443. 26 text-figures and photographs.

(1) Sumner's work, comprising three years of intensive field study, can be compared only with Stoddard's. His conclusions published in these two papers form a worthy successor to Stoddard's book on the bob-white quail. Nearly every conceivable aspect of the ecology of the California quail has received some attention. The food and feeding habits have been accurately determined by the examination of 170 stomachs coupled with field studies; mortality rates, covey range and movements and population increase have been studied with the help of an intensive banding scheme and counts on one area; while a careful analysis of the make up of optimum environments for quail has made it possible to give definite suggestions for improvements in conservation and management.

(2) Errington and Hamerstrom have made a special study, lasting over six winters, of the survival and mortality of bob-whites under different conditions in Iowa and Wisconsin. Repeated censuses on sample areas, together with an analysis of the environment, show that different areas have very different carrying capacities for bob-white and that the carrying capacity remains (within limits) fairly constant and independent of weather conditions so long as the make up of the environment is unchanged. Special attention has been devoted to the mortality due to predators and the facts indicate that in most habitats predators will help to reduce the winter population of bob-whites to a figure near the carrying capacity, but for populations at or below that level the action of predators is less significant. Suggestions are given for the control of the environment and raising the carrying capacity by creating an optimum interspersion of cover and feeding grounds.

A. D. MIDDLETON.

SHORT REVIEWS

J. S. R. Chard (1936). *British animal tracks.* 80 pp. C. Arthur Pearson, Ltd., London. Price 3*s.* 6*d.*

Scale diagrams of footprints and trails of 32 species of native British mammals are simply and clearly drawn. Special emphasis is given to features distinguishing one wild species from another or from a domestic species. The author restricts the scope of this work mainly to the narrower meaning of tracking—interpretation of footprints. Certain other features are introduced, but no mention is made of specific characteristics of excreta. Particularly when making rapid faunal surveys, it is droppings, rather than footprints, that are the more frequent and reliable indices of presence of a species of mammal. A book on the droppings of British mammals would be a most valuable companion volume to the present, especially if planned on the same excellent lines.

D. H. CHITTY.

H. Gilbert Carter (1936). *British trees and shrubs, including those commonly planted: a systematic introduction to our conifers and woody dicotyledons.* 291 pp. Clarendon Press, Oxford. Price 12*s.* 6*d.*

This is a compact and attractive book, although it has no illustrations. The taxonomic descriptions are lucid and well arranged; but the special advantage of the book is its notes, about the country of origin, the general habits, and the special interest or uses of each species. The last are the distillation of a very wide knowledge. Here is an example of an English shrub, the spindle (*Euonymus europaeus*): "In Britain it is common in the chalk scrub, and is a characteristic shrub of our woods on chalky boulder-clay and also of the Ash Woods on the older limestones. 'The larva of *Phalaena castralis* yearly devours the leaves. The very rigid wood is used for skewers, spindles, and distaffs. The fruit kills sheep; powdered it destroys lice. The aril is violently purgative. A lye of the fruit makes the hair bright and shining. Charcoal better than that of hazel for drawing. An excellent shrub for hedges in gardens.' *Euōnymos* in Pliny, *εὐώνῦμος* in Theophrastus. The word means 'of good name, or honour', and is perhaps applied ironically because of the poisonous properties of the plant intended."

CHARLES ELTON.

A. Landsborough Thomson (1936). *Bird migration: a short account.* 224 pp., 10 text-figures, 6 plates. H. F. & G. Witherby, Ltd., 326 High Holborn, London, W.C. 1. Price 5*s.*

This is a small book by a great expert, who has selected with skill the essential ideas and facts about migration, illustrating them with good sketch-maps and some very attractive photographs of bird ringing and trapping, and country seen from the air. The author mentions the latest results of observation and experiment, though he does not go deeply into physiological questions. About the origin of migration he is cautious, being mainly concerned to drive home the complexity of the whole subject, and to show how far modern methods have succeeded in penetrating it. There is a list of selected references, and a good index.

CHARLES ELTON.

Edmund Sandars (1937). *A beast book for the pocket: the vertebrates of Britain, wild and domestic, other than birds and fishes.* 378 pp. (size $4 \times 5\frac{7}{8}$ in.) and numerous sketch-maps, text-figures and coloured plates. Oxford University Press. Price 7*s.* 6*d.*

There has long been need for a reliable popular book on British mammals, since the only thoroughly scientific text-book (Barrett-Hamilton and Hinton's *British Mammals*) was never completed, and is in any case rather large for the ordinary person. Step's *Animal life of the British Isles* is rather too general and vague. The present pocket manual is a brilliant effort of compilation. All the important species are treated separately, and their rarer allies (e.g. island forms) mentioned. The distribution, habitats, structure, life, food, gait, voice, etc. are briefly summarized. Besides including reptiles and amphibians, the author boldly embarks on domestic animals as well, since these are more prominent in our landscape than wild species. The author's thumbnail sketch maps of distribution are useful, though not always (as with the muskrat) very reliable in detail. His coloured pictures of nearly all the important species are often successful; but there are a few which have deplorably misleading colours (e.g. long-tailed field-mouse, which has no resemblance to fact). It would be better in future editions either to use line drawings for the difficult ones, or improve them. Apart from this question, the book is an excellent piece of work and will be, one hopes, widely used.

CHARLES ELTON.

J. E. Forrest, A. R. Waterston & E. V. Watson (1936). *The natural history of Barra, Outer Hebrides. The results of a scientific expedition organised by the Biological Society of the University of Edinburgh, 1–14 July* 1935. Proc. R. Phys. Soc. Edinburgh, 22: 241–96.

This expedition extensively collected land, freshwater and marine animals and plants, including fungi, lichens, and seaweeds. The results are given in a series of 30 reports by various specialists, preceded by a general account of topography and a rough ecological description of vegetation. The animals were not studied by communities, so that the results have chiefly a distribution value, although general habitat notes are given for many species. A number of new distribution records were made, some new for Scotland. *Gammarus pulex* was absent from streams, where *G. duebeni* occurred instead. The estuarine *Neomysis vulgaris* occurred in a practically freshwater loch. The freshwater sponge, *Heteromyenia ryderi*, hitherto known only in N. America, Ireland and Mull, was found in Barra lochs. It is a pity that such a large survey was not so organized as to give more data of ecological value; it affords, however, a useful basis for more intensive community studies.

CHARLES ELTON.

Marion I. Newbigin (1936). *Plant and animal geography.* 298 pp. and 39 text-figures. Methuen and Co. Ltd., 36 Essex Street, London, W.C. 2. Price 12*s.* 6*d.*

The late author of this book was an authority on geography, especially that of plants, and had travelled, more than most people, in the regions she describes. The book deals with the general biological interrelations of plants with their environments, gives a general review of plant communities, and then discusses, still in a very general way, animal adaptation. A large section is concerned with zoogeographical realms, and here the treatment is rather diffuse, and certainly does not contain the best results of later European research. The animal ecologist will, however, find many features of great use in the accounts of the distribution of soil, climate and plant communities throughout the world. There are some useful maps.

CHARLES ELTON.

NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals, large and small. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Copies of these abstracts, gummed, and cut down to a width suitable for five-inch index cards, are issued free with the *Journal*. They can also be obtained separately by non-subscribers, from the Cambridge University Press, Fetter Lane, E.C. 4, or through a bookseller, price 3*s*. 6*d*. per annum post free (about 300 notices, in two sets, May and November).

Abstracting has been done by H. F. Barnes, J. R. Carpenter, D. H. Chitty, C. Elton, F. Evans, J. Ford, B. M. Hobby, and A. D. Middleton.

1. ECOLOGICAL SURVEYS AND HABITAT NOTES

(*a*) Marine and brackish

1. Kitching, J. A. (1935). "An introduction to the ecology of intertidal rock surfaces on the coast of Argyll." Trans. Roy. Soc. Edinburgh, 58: 351–74.

The ecology of the plants and animals on a rock shore free from boulders, and open to severe wave action, whose effect on zonation is discussed. Splash and mechanical shock are considered the most important factors in wave action, which enables an upward extension on the shore of certain littoral plants and animals.

2. Brady, F. (1932). "Notes on the distribution of *Macoma baltica* (L.) and *Scoloplos armiger* (O. F. Müller)." Proc. Univ. Durham Phil. Soc. 9: 31–9.

Notes on the distribution of 11 marine animals in 12 habitats in Budle Bay, N.E. Northumberland, with a description of the habitats.

3. Frost, W. E. (1934). "The occurrence and development of *Euphausia krohnii* off the south-west coast of Ireland." Proc. R. Irish Acad. B, 42: 17–40.

A description of the life stages and distribution of this Crustacean, including notes on its reproductive cycle. The time between metanauplius and adult and the number of generations per year are still unknown.

4. Stephen, A. C. (1935). "Notes on the intertidal fauna of North Uist." Scottish Nat.: 137–42.

The exposed sandy shores have little life, and no Molluscs. The sheltered sandy shores, behind islands have two abundant Molluscs (*Macoma baltica* and *Cardium edule*) together with two other species; the worm *Arenicola marina* abundant, with some other species; but *Tellina tenuis*, a Mollusc abundant elsewhere in Scotland was very rare. Notes on tidal zonation are given.

5. Bagnall, R. S. (1935). "Our shore-dwelling Pauropods." Scottish Nat.: 143–5.

Notes on Thysanura from tidal areas.

6. Nichol, E. A. T. (1936). "The brackish-water lochs of North Uist." Proc. Roy. Soc. Edinb. 56: 169–95.

An account of the ecological conditions, plants and animals found on the strand and in 7 brackish lochs in North Uist, Outer Hebrides. The lochs are at different levels and have salinities varying with the comparative degrees of tidal inflow. Animals listed include 59 marine, 24 freshwater, 25 brackish water, and 5 euryhaline species. A comparison of distribution of 7 species of Mollusca with reference to salinity in the lochs and to a Johanssen's study in the Randersfjord shows discrepancies which cannot be explained by calcium concentration.

7. Nichol, E. A. T. (1936). "The fauna of Loch Bee." Scottish Nat.: 131–4.

The ecological conditions, animals and plants of Loch Bee, South Uist, Outer Hebrides. Four stations of different histories in their connexion with the sea were studied; samples were taken from sand, shell, and mud bottoms. The fauna is very similar to the lochs of North Uist (see **6** above).

8. Southern, R. (1936). "Turbellaria of Ireland." Proc. R. Irish Acad. B, 43: 43–72.

Occurrence and habitats of 103 species of free-living flatworms: land (5), freshwater (26), marine (70), marine and freshwater (2).

(*b*) Freshwater

See also **6, 7, 8, 16, 69**

9. Moon, H. P. (1936). "The shallow littoral region of a bay at the north-west end of Windermere." Proc. Zool. Soc. Lond. 491–515.

A sheltered portion of the lake edge rich in silt is described, with notes on the physiographic and physical elements of the habitats. To the depth of 2·5 ft. four habitats are recognized: vertical rock walls, stony shores covered with silt, *Phragmites* and *Scirpus* swamps free from stones, and sandy shores. Below 2·5 and to 5 ft. is found a muddy gravel bottom covered with *Littorella*, where the animal population decreases both in numbers and species. The reed swamp animals show a tendency towards succession to pond populations. A comparison of a less silted area in Windermere (see *J. Anim. Ecol.* (1934) 3: 8) with regard to populations and the environment is made and the importance of microhabitat differences shown. There are faunal lists for the habitats studied.

10. Smart, J. (1936). "Notes on the Simuliidae occurring at Fortingal, Perthshire." Scottish Nat.: 22–6.

General habitats of 7 species of *Simulium*, according to stream types.

11. Balfour-Browne, F. (1936). "The aquatic Coleoptera of north and south Somersetshire." Trans. Soc. Brit. Ent. 3: 129–53.

An account of 152 species of beetles with a table of habitats.

12. Dyson, J. E. B. & Lloyd, Ll. (1936). "The distribution of the early stages of *Metriocnemus longitarsus* Goet. (Chironomidae), in sewage bacterial beds." Proc. Leeds Phil. Lit. Soc. 3: 174–6.

In a sewage bed at Leeds, larvae and pupae found to be abundant at 2 in. and larvae at from 3–6 ft. below the surface among the filter pebbles.

13. Blackburn, E. P. (1934). "A survey of the land and fresh water Mollusca of Northumberland and Durham." Trans. Northern Nat. Union, 1: 139–86.

A description of the physiographic characteristics of the subdivisions of the area, with notes on the changes in the Molluscan fauna in the last 100 years; also a brief account of sub-fossil shells found. 136 spp. listed.

14. Boycott, A. E. & Oldham, C. (1936). "The Mollusca of the western parts of the Shropshire Union Canal." Northw. Nat. 11: 217–27.

The canal affords a gradual change of habitat from definitely calcareous waters to those deficient in lime. Of the 40 species taken, 6 are new to Wales. Full lists of species and distribution.

15. Griffiths, B. M. & Cocks, F. E. (1931). "The Rotifers of the Northumberland plankton." Trans. Northern Nat. Union, 1: 45–7.

In 17 bodies of water in the Northampton region are recorded 49 spp. of Rotifers.

(c) Land

See also **8**

16. Howard, H. J. (1935). "The zoology of Norfolk." Rep. British Ass. (Appendix): 36–49.

A list, admittedly incomplete, of the fauna of county Norfolk with comments on occurrence.

17. Campbell, B. (1935). "Notes on the birds of Loch Ard Forest." Scottish Nat.: 151–9.

Survey of bird communities on water, cultivated areas, woodland (deciduous and coniferous) and moorland, consisting mainly of scattered notes on occurrence and habits, and a sketchy list of birds in each habitat.

18. Thornley, A. (1936). "A provisional list of Cornish insects. Part III.—Diptera (Acalyptratae)." Trans. Soc. Brit. Ent. 3: 155–71.

Gives localities for 356 species representing 34 families of flies.

19. Fisher, R. C. (1936). "Insects attacking the timber of English oak." Forestry, 10: 47–57.

Descriptions and habits of many species on green and old oak timber, with photographs.

20. F....., L. T. (1936). "Micro-collecting in September." Ent. Rec. 48: 100.

Useful hints on breeding Lepidoptera from larvae feeding in the seed heads of various plants. See also "**E. E. E. F.**" (**1936**), *ibid.* 48: 101.

21. Fordham, W. J. (1936). "Some more insect Jacobites." Naturalist: 132.

Insects living on or visiting *Senecio jacobaea*.

22. Ford, L. T. (1936). "*Melissoblaptes bipunctanus*, Zeller 1848." Ent. Rec. 48: 93–4.

This local Galleriid moth is recorded from sandhills between Sandwich and Deal. The larva constructs surface tunnels of silk among the moss *Brachythecium albicans*, extending them when necessary to reach fresh food. The nearly full-fed larva lives in a vertical silk-lined tube extending four or more inches below the surface.

23. Wakely, S. (1936). "Notes on the plume moths." Proc. Trans. S. Lond. Ent. Nat. Hist. Soc. 1935–6, 97–9.

Habitats and breeding notes on a few of the 34 British species.

24. Syms, E. E. (1936). "Some notes on the biology of *Chrysopa septempunctata*, Wes." Proc. Trans. S. Lond. Ent. Nat. Hist. Soc. 1935–6, 52–4.

A popular account of the life-history of a green lacewing.

25. Donisthorpe, H. St J. K. (1936). "A preliminary list of the Coleoptera of Windsor Forest." Ent. Mon. Mag. 72: 210–19, 260–7.

26. Coulson, F. J. (1936). "A few remarks upon British Rhynchophora." Proc. Trans. S. Lond. Ent. Nat. Hist. Soc. 1935–6: 100–7.

Excellent notes for the collection of weevils, with habitat groupings.

27. Cook, J. H. (1936). "A contribution towards a study of *Calosoma inquisitor* L. (Coleopt., Carabidae)." Trans. Soc. Brit. Ent. 3: 79–114.

A review of the literature with an account of the distribution and anatomy of a beetle of considerable importance in the control of the defoliating caterpillars of oaks.

28. Fidler, J. H. (1936). "On the first instar larvae of some species of *Otiorrhynchus* found on strawberries, with notes on their biology." Bull. Ent. Res. 27: 369–76.

There are four species of weevils, which commonly, in both the larval and the adult stage, cause damage to strawberry plants; a brief description of their biology is given; all are usually parthenogenetic, but it is uncertain if they can reproduce sexually, since males have not yet been recorded. They usually have one generation in the year, oviposit in mid-summer and over-winter as well-developed larvae. In two species adults may emerge in the late summer and having hibernated as adults, lay eggs in the early spring.

29. Miles, H. W. (1936). "On the biology of certain species of *Holcocneme* Kon. (Hymenoptera-Symphyta)." Ann. Appl. Biol. 23: 781–802.

Deals with *H. caeruleocarpa* on *Salix* and *Populus*, *H. lucida* on *Prunus*, *H. crassa* on *Salix*, *Populus* and *Rumex* and *H. erichsoni* on *Larix*.

30. Miles, H. W. (1936). "On the biology of *Emphytus cinctus*, L., and *Blennocampa waldheimi*, Gimm. (Hym., Symphyta). Bull. Ent. Res. 27: 467–73.

These sawflies cause injury to Rosaceae.

31. Aitkins, A. E. (1936). "The 'spruce cone bug', *Gastrodes abietis* Linn. (Hemiptera-Heteroptera: Lygaeidae)". Ent. Mon. Mag. 72: 139–49.

In addition to descriptions of the various stages, the distribution and notes on feeding habits and damage are given.

32. Aitkins, A. E. (1936). "Spruce cone bug, *Gastrodes abietis*, L." Scot. Forestry J. 50: 44–9.

Description, life history and British distribution map.

33. Cameron, A. E. (1936). "*Adelges cooleyi* Gillette (Hemiptera, Adelgidae) of the Douglas fir in Britain: completion of its life cycle." Ann. Appl. Biol. 23: 585–605.

The *fundatrix vera* and *gallicolae* generations have been discovered for the first time and their development followed.

34. Cohen, M. (1936). "The biology of the *Chrysanthemum* leaf-miner, *Phytomyza atricornis* Mg. (Diptera: Agromyzidae)." Ann. Appl. Biol. 23: 612–32.

A good detailed study from many aspects. Very heavy parasitism by an unidentified Braconid and many examples of a Chalcid which is probably a hyperparasite.

35. Taylor, E. (1935). "Notes on Oniscoidea (woodlice) with a preliminary list of the Oxford species." Proc. Ashmolean Nat. Hist. Soc. for 1934: 19–22.

14 species recorded.

36. Taylor, E. (1936). "Report on Oniscoidea (woodlice)." Proc. Ashmolean Nat. Hist. Soc. for 1935: 16–17.

3 additional species for the Oxford district.

37. Swan, D. C. (1936). "Berlese's fluid: remarks upon its preparation and use as a mounting medium." Bull. Ent. Res. 27: 389–91.

An excellent medium for mounting small Arthropods.

38. B....., P. B. (1936). "Mollusca in fir and larch woods." Vasculum, 22: 154.

"It is a very rare thing to find any mollusca in such woods." Gives records of *Limax maximus*, *L. arborum*, *Arion circumscriptus* and *A. subfuscus* in such localities.

39. Waterston, A. R. (1935). "The land planarians of the British Isles." Scottish Nat.: 103–9.

Known distribution and habits of the three British species of *Rhynchodemus*, with descriptions of worms and a bibliography.

(*d*) Small islands

See also **4, 6, 71, 90, 143**

40. Vevers, H. G. (1936). "The land vegetation of Ailsa Craig." J. Ecol. 24: 424–45.

This ecological survey includes references to grazing effects of rabbits, sheep and goats; manuring effects of sea birds; seed carriage by land birds.

41. Gladstone, H. S. (1937). "Dr Charcot and the birds of Rockall." British Birds, 30: 251–3.

Records some birds seen, with photographs of the island.

42. Ainslie, J. A. & Atkinson, R. (1937). "On the breeding habits of Leach's fork-tailed petrel." British Birds, 30: 234–48.

Studied continuously for a month on island of North Rona. Estimated population in 1936 was 380 breeding pairs.

43. Lewis, S. (1936). "Birds of the island of Steep Holm." British Birds, 30: 219–23.

Full list of breeders and visitors compiled from records and literature.

44. Baxter, E. V. (1935). "The breeding song thrushes of Shetland." Scottish Nat.: 110

Shetland thrushes belong to the Continental subspecies (*Turdus ericetorum philomelus*).

45. Gilles, W. S. (1936). "Notes on the Lepidoptera of Skye." Ent. Rec. 48: 94–5.

Short notes concerning the more interesting species observed during a series of summer visits, extending over a period of twenty years.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

See also Section 4, for parasites

46. Griffin, F. J., Sherborn, C. D. & Marshall, H. S. (1936). "A catalogue of papers concerning the dates of publication of natural history books." J. Soc. Bibl. Nat. Hist. 1: 1–30.

An invaluable guide to the vast amount of bibliographical research published during the present century, and scattered widely through scientific periodicals.

47. Harrison, J. W. Heslop (1932). "The autumnal moths of the genus *Oporinia* Hb., with an account of a new American species." Trans. Northern Nat. Union, 1: 111–36.

Taxonomical description, variations, and habitats of the 4 British spp. of this Geometrid genus.

48. Burr, M. (1936). "British grasshoppers and their allies. A stimulus to their study." London.

A very useful guide for the determination of species; with keys, short descriptions, 6 plates, 56 text-figures and 40 distribution maps. (See review in J. Anim. Ecol. (1937), 6: 200–1.)

49. Walton, G. A. (1936). "A new species of Corixidae, *Sigara pearcei* (Hemipt.) from Ireland; together with descriptions of its closely related species." Trans. Soc. Brit. Ent. 3: 33–47.

Includes key to British species of these water-bugs.

50. Macfie, J. W. S. (1936). "Two new species of Ceratatopogonidae (Diptera) from the wings of dragonflies." Proc. R. Ent. Soc. Lond. B, 5: 62–4.

The remarkable genus of flies, *Pterobosca*, has not previously been discovered in Europe; a new species, *Pterobosca paludis*, is described from Wicken Fen.

51. Pearman, J. V. (1936). "The taxonomy of the Psocoptera: preliminary sketch." Proc. R. Ent. Soc. Lond. B, 5: 58–62.

Summary of revised classification.

52. Bagnall, R. S. (1935). "Contributions towards a knowledge of the Scottish Onychiuridae (Collembola), I." Scottish Nat.: 111–17.

Records and describes 7 species (5 said to be new) of these small white springtails from Britain.

53. Hull, J. E. (1932). "Nomenclature of British Linyphiid spiders: a brief examination of Simon's French catalogue." Trans. Northern Nat. Union, 1: 104–10.

Corrections of the names of British Linyphiids given by Simon in the posthumously published *Arachnides de France*.

54. Hull, J. E. (1931). "Terrestrial Acari of the Tyne province...." Trans. Northern Nat. Union, 1: 37–44.

A taxonomic account of the British Tyroglyphidae (mites) with keys to 13 genera and 35 spp.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS

See also **40, 110, 111, 126, 127, 128, 145**

55. Renn, E. (1936). "Persistence of the eel-grass disease and parasite on the American Atlantic coast." Nature, 138: 507–8.

A brief summary of the eel-grass beds between Cape Cod and Barnegat Bay, New Jersey, and the universal presence of the fungus parasite *Labyrinthula*.

56. Watt, A. S. (1936). "Studies in the ecology of Breckland. I. Climate, soil and vegetation." J. Ecol. 24: 117–38.

Includes discussion on effects of man and rabbits on vegetation of Breckland in Norfolk.

57. Von Schiller, P. (1937). "Vergleichende Untersuchungen über Bewegungssehen." Biol. Rev. 12: 116–53.

The movement-vision of man and animals is compared. Movement-vision occurs when a change in the light pattern produces a reaction whose direction is determined by that change. This vision is either real, induced or kinematoscopic. It was first demonstrated experimentally in Decapods (Doflein), later in bees (Wolf), fowls and rats. The complex eye of Arthropods prevents kinematoscopy. Uexküll's school proved that movements seemed twice as rapid to the fighting fish *Betta* as to man. The physiological theories of movement-vision by Hertz and Köhler are discussed, the latter being accepted with a slight modification.

58. Jourdain, F. C. R. (1936). "On the winter habits of the green woodpecker (*Picus viridis virescens*)." Proc. Zool. Soc. Lond. 251–6.

The green woodpecker has a working day of 8–9 hours in the winter, usually entering its hole by 4.30 p.m. The sexes roost apart.

59. Marples, G. (1936). "Woodpecker nesting holes and the compass." British Birds, 30: 84–6.

Out of 123 nesting holes of green woodpecker, 71 had N. aspect, 28 S. and 24 E. or W.

60. Morley, A. (1936). "The winter behaviour of moor-hens." British Birds, 30: 120–4.

Courtship and territorial behaviour in Oct.–Dec.

61. Pounds, H. E. (1936). "Notes on the flight of the sparrow-hawk." British Birds, 30: 183–9.

Notes four kinds of flight, with detailed field observations.

62. Harrisson, T. H. & Buchan, J. N. S. (1936). "Further notes on a field study of the St Kilda wren (*Troglodytes troglodytes hirtensis* Seeb.), with especial reference to its nest habits and song." Scottish Nat.: 9–21.

Average feeding visits to young 10–13 per day of 13½ hours. Notes on nest materials, etc. Singing diminished after end of July, and increased again in mid August. There is an average maximum frequency of song at noon and evening. Notes are described, speed of flight (estimated to spend 2% of time in air during day), and plumage.

63. Mansbridge, G. H. (1936). "A note on the resistance to prolonged cold of some insect pests of stored products." Proc. R. Ent. Soc. Lond. A, 11: 83–6.

Resistance to cold is probably a large factor in determining the prevalence of these insects and nearly all the survivors of cultures left in an unheated building through two English winters are common pests in this country, while the remaining species have seldom become serious pests, and then only in heated buildings. A list is given of species able to survive a winter when the temperature falls 2° C. below zero.

64. **Thomsen, M. & Hammer, O. (1936).** "The breeding media of some common flies." Bull. Ent. Res. 27: 559–87.

An account of investigations on a number of very common European species including the house-fly and the stable-fly, undertaken in Denmark.

65. **Mellanby, K. (1936).** "Humidity and insect metabolism." Nature, 138: 124–5.

Experiments with mealworms at various temperatures and humidities show that rate of metabolism (as indicated by the using of food reserves and consequent loss of dry weight) and the amount of CO_2 produced are dependent on temperature only. Citing other experiments, it is concluded that an increase of metabolism rates does not aid an insect to withstand desiccation.

66. **Mellanby, K. (1936).** "To measure the humidity of the soil atmosphere." Bull. Ent. Res. 27: 287.

An accurate and simple method is described.

67. **Scott, W. N. (1936).** "An experimental analysis of the factors governing the hour of emergence of adult insects from their pupae." Trans. R. Ent. Soc. Lond. 85: 303–29.

In the insectary the moth *Ephestia kühniella* shows a diurnal rhythm of emergence with a maximum in the evening. This rhythm is closely related with the diurnal temperature rhythm. The maximum emergence occurs shortly after the temperature begins to fall. The rhythm is continued in a constant-temperature room, but is not so well defined. The rhythm is inherited. The time of maximum emergence may be changed by altering the time of maximum temperature. Light above a certain intensity inhibits emergence.

68. **Mansbridge, G. H. (1936).** "Experiments on the resistance of the flour moth (*Ephestia kühniella* Zell.) to abnormally high temperatures." Ann. Appl. Biol. 23: 803–21.

Eggs from different pairs of moths may have widely different degrees of resistance, larvae are much less resistant than eggs, pupae are more resistant than feeding larvae and adults are the most susceptible stage to heat.

69. **Hinton, H. E. (1936).** "Notes on the biology of *Dryops luridus* Erichson (Coleoptera, Dryopidae)." Trans. Soc. Brit. Ent. 3: 67–78.

These beetles frequent stagnant water; when submerged they are *entirely* surrounded by a film of air; during the day they usually remain in the water, at night they come to the surface and fly about; in the laboratory they feed on fresh and partly decayed leaves of water mint; copulation takes place both in and out of the water; the eggs are normally inserted in plant tissue; in the laboratory eggs were laid under water; larvae have been found in damp sods away from water; the egg and larva are described.

70. **Cameron, A. E. (1934).** "The life-history and structure of *Haemotopota pluvialis*, Linné (Tabanidae)." Trans. Roy. Soc. Edinburgh, 58: 211–50.

An account of the biology, including digestion, reproduction, and development, and the anatomy of the larval instars and adults. The significance of intermittent blood-feeding and periodic oviposition is discussed.

71. **Evans, A. C. (1936).** "The physiology of the sheep blow-fly *Lucilia sericata* Meig. (Diptera)." Trans. R. Ent. Soc. Lond. 85: 363–77.

The effect of temperature and humidity on all stages in the life-history of the insect is discussed. Micro-organisms play no part in the digestion of food in the gut of the larvae: their importance lies in the synthesis of an accessory growth factor and the liquefaction of the food. The age and diet of flies are important factors in their reaction to humidity. The attraction or repulsion of decomposing matter for flies depends on the relative amounts present of certain substances. Bacterial activity in the fleece is the chief cause of flies ovipositing on living sheep.

72. Cunliffe, N. (1936). "Studies on *Oscinella frit* Linn. Inheritance of resistance of oats to attack by the fly and the combination of resistance with other characters of agricultural importance." Ann. Appl. Biol. 23: 822–44.

Resistance is shown to be an inheritable character and agricultural quality and resistance to attack are not incompatible. Wet weather conditions during the flight of the fly have a very marked effect in limiting the extent of damage. Varietal differences in extent of attack may be due to varietal differences in crude fibre production or deposition of silica.

73. Cott, H. B. (1936). "The effectiveness of protective adaptations in the hive-bee, illustrated by experiments on the feeding reactions, habit formation, and memory of the common toad (*Bufo bufo bufo*)." Proc. Zool. Soc. Lond. 111–33.

33 toads learned to avoid bees within one week; a single experience was sufficient for 10 of them. This memory was retained for a fortnight. Bees may be thus well-defended against predatory attack by vertebrates.

74. Sandeman, R. G. C. C. (1936). "Notes on the habits of *Vespa vulgaris* and *V. germanica* (Hymenoptera)." Proc. R. Ent. Soc. Lond. A, 11: 88–90.

Notes on nesting, general habits and hibernation.

75. Walton, G. A. (1936). "Oviposition in the British species of Notonecta (Hemipt.)." Trans. Soc. Brit. Ent. 3: 49–57.

Four species of this genus of water-bug occur in Britain; one normally deposits its eggs in incisions made by its ovipositor in plant tissues; two normally do likewise, but sometimes affix their eggs to solid supports and the surfaces of plants; the fourth always lays on a solid support, never on soft plants.

76. Poole, H. H. & Atkins, W. R. G. (1935). "The measurement of the current generated by rectifier photo-electric cells." Sci. Proc. R. Dublin Soc. 21: 133–9.

The description of a modification of the Campbell-Freeth circuit system for the measurement of the current generated by rectifier cells, enabling accurate measurements at sea.

77. Poole, H. H. & Atkins, W. R. G. (1934). "Some measurements of the brightness of various parts of the sky by means of a rectifier photo-electric cell." Sci. Proc. R. Dublin Soc. 21: 1–8.

Describes the use of the Bergmann selenium cell, and the results obtained at various azimuths in June.

78. Poole, H. H. & Atkins, W. R. G. (1936). "The standardisation of photo-electric cells for the measurement of energy." Sci. Proc. R. Dublin Soc. 21: 363–79.

79. Scourfield, D. J. (1934). "The Linnéscope." School Nature Study, 29: 46–7.

A contrivance consisting of a box, blackened on the inside, in which a magnifying lens is inserted at one end. An adjustable moving stage provides focusing. Recommended for outdoor work by amateur biologists and by school classes which are not experts at handling a hand lens. Obtainable from Messrs W. Watson & Sons, Ltd., 313 High Holborn, London, W.C. 1, for 15*s*.

4. PARASITES

See also **34, 71, 113**

80. Thompson, G. B. (1936). "The parasites of British birds and mammals. IX. A bibliography of the papers containing records of Mallophaga (biting-lice) from birds and mammals." Ent. Mon. Mag. 72: 159–61.

81. Thompson, G. B. (1936). "The parasites of British birds and mammals. X. Records of Mallophaga from birds." Ent. Mon. Mag. 72: 224–8.

82. Britten, H. (1936). "A short-eared owl and its passengers." Northw. Nat. 11: 48.

On a short-eared owl (*Asio flammeus*) were one species of biting louse and three species of feather mites, two of which came from a moorhen (*Gallinula chloropus*) which the owl had eaten.

83. Hull, J. E. (1934). "Concerning British Analgidae (feather-mites)." Trans. Northern Nat. Union, 1: 200–6.

A list of 44 British genera, with notes on their avian hosts. 4 new genera proposed and one new species (*Avenzoaria ochropoda*) described.

84. de Montmorency, H. B. (1935). "Some observations on *Filaroides mustelarum*, a little-known nematode, occurring in stoats and weasels." Scottish Nat.: 99–101.

These worms live in the frontal sinuses of the skull, extending also to the nasal sinuses. It is widespread, being recorded from Scotland, Ireland, England, and probably U.S.A. It causes lesions in the skull.

85. Richards, O. W. (1936). "Breeding records of Hymenoptera and Diptera." J. Soc. Brit. Ent. 1: 162–4.

Includes records of parasites with complete data.

86. Jackson, D. J. (1935). "Further notes on parasites of the magpie moth (*Abraxas grossulariata* L.) in Scotland." Scottish Nat.: 89–98.

87. Morley, C. (1936). "Notes on Braconidae: XV. Microgasterinae." Entomologist, 69: 39–42, 64–7, 90–4, 115–19, 140–2, 161–3, 187–91, 209–15.

Contains many host insect references. Lists of Lepidopterous hosts as well as list of hyper-parasites and commensals are given in concluding part (pp. 213–15).

88. Kerrich, G. J. (1936). "The Ichneumonoidea of Wicken Fen: Corrigenda and addenda." Trans. Soc. Brit. Ent. 3: 61–6.

With these corrections and additions to **G. L. R. Hancock's** list in **J. S. Gardiner (1925)**, "The natural history of Wicken Fen," Part 2, Cambridge, the number of species on the list for Wicken Fen stands at 354 (Ichneumonidae 290, Braconidae 62, and Evaniidae 2).

89. Hobson, R. P. (1936). "Sheep blow-fly investigations. III. Observations on the chemotropism of *Lucilia sericata* Mg." Ann. Appl. Biol. 23: 845–51.

Attractions for the fly of putrefying substances, when placed on sheep, seems to be largely due to the presence of indole, scatole, and ammonium carbonate. Dilute solutions of these substances attract females to oviposit. Individual sheep vary in their attractiveness and this can be measured with solutions of indole and ammonium carbonate. Further reference **R. P. Hobson**, "On the chemistry of the fleece with reference to the susceptibility of sheep to blow-fly attack," *ibid.* 852–61.

90. MacLeod, J. (1936). "A new blowfly attacking sheep in western Scotland." Nature, 138: 467–8.

Phormia terrae-novae R.-D., closely related to *Phormia regina*, the principal sheep blow-fly of North America, is recorded for the first time on sheep. It occurred in Mull and western Argyllshire on blackfaced sheep of the blackfaced variety in long wool, causing "strike". It is concluded that this species as well as *Lucilia sericata* must be considered as causes of strike, at least in Scotland.

91. Taylor, J. N. (1934). "Worms of the genus *Mermis* parasitic on the yellow ant. (*Acanthamyops flavus* F.)." Proc. Cotteswold Nat. Field Club, 25: 183–5.

Males of this ant are found to be parasitized as well as the females. Larval existence of *Mermis* is spent in the abdomen of the ant adults, the rest of the life cycle being completed in damp soil. The generic name of the ant should be *Acanthomyops*.

92. Petch, T. (1934). "Report on Fungi occurring on flies collected in the Pin Hole Cave." Rep. British Ass.: 255–6.

5 spp. of Fungi, one a new species, on flies (names not given) in a cave in Derbyshire.

93. Scourfield, D. J. (1936). "The occurrence of a minute fungus on a free-swimming Alga (a Chytrid on *Chlorogonium*) in an Epping Forest pond." Essex Nat. 25: 120–3.

A new English record of *Phlyctidium chlorogonii* found in Nov. 1934, on a member of the Volvocales. Chytridae are said to be typically aquatic Fungi, and have been found on floating pollen grains, on small aquatic animals, and on other aquatic fungi such as *Saprolegnia*. (Illustrated plate of different stages of development.)

5. FOOD AND FOOD-HABITS

See also **62, 73, 130**

94. Campbell, J. W. (1936). "On the food of some British birds." British Birds, 30: 209–18.

Quantitative analyses of stomach contents of about 370 birds, including rooks, jackdaws, jays, geese, plovers, snipe, woodcock, pheasants and partridges. Most of the material was collected from North Uist (Outer Hebrides) and Essex.

95. Collinge, W. E. (1936). "The food and feeding-habits of the coot (*Fulica atra* Linn.)." Ibis, 6: 35–9.

Careful observation and stomach analyses prove the coot's feeding habits harmless to fisheries. 84 % of the food is vegetable matter.

96. Mitchell, M. (1936). "Herring-gulls feeding on larvae of moths." British Birds, 30: 92.

Young gulls fed largely on larvae of *Cerapteryx* (*Charaeas*) *graminis* L. on Puffin Island, Anglesey.

97. Holmes, P. F. (1937). "Gulls taking ants off surface of lake." British Birds, 30: 261.

During marriage flight of *Acanthomyops flavus* on Windermere, gulls (*Larus f. graellsii, ridibundus* and *argentatus*) ate them on surface of water.

98. Höhn, O. E. (1936). "Food of kestrel and possible seed-dispersal." British Birds, 30: 192.

Kestrel's nest contained remains of mice, voles, rats and sparrows. Seeds from prey's stomachs found in kestrel pellets.

99. Brown, R. H. (1936). "The food of young lapwings." British Birds, 30: 134.

Caterpillars, earthworms, wireworms, flies and fly grubs.

100. Campbell, J. W. (1936). "Spotted flycatcher, great tit and gulls taking moths." British Birds, 30: 172.

The gulls were taking *Hepialus fusconebulosa.*

101. Britten, H. (1936). "Birds and galls of *Mayetiola ventricola* Rubs." Northw. Nat. 11: 269.

Skylarks and black-headed buntings pulled these galls from the grass (*Molinia caerulea*).

102. Wadsworth, R. V. (1936). "*Ephestia* larvae eating dead larvae of their own species." Entomologist, 69: 159.

103. Hobby, B. M. (1936). "Dragonflies and their prey." Proc. R. Ent. Soc. Lond. A, 11: 101–3.

Additional records and references, chiefly British.

104. Edwards, F. W. (1936). "Midges attacking caterpillars." Entomologist, 69: 192.

Forcipomyia pallida Winnertz feeding on Geometrid larvae. Further reference in **T. Bainbrigge Fletcher**, *ibid.* 192.

105. Cowley, J. (1936). "Notes on British Odonata in 1934 and 1935." Entomologist, 69: 149–53.

Contains a summary of the information available concerning midges (Ceratopogonids) attacking Odonata. Further reference in **J. Cowley**, *ibid.* 192.

106. Hey, G. L. (1936). "A note on wireworm injury to fruit-trees." Ent. Mon. Mag. 72: 229–30.

Wireworms feeding on the bark and the wood of the stem of apple trees planted the previous year on what had been pasture for at least 30 years.

6. ANIMAL POPULATIONS

See also **9, 13, 42, 141, 144**

107. Ritchie, James (1934). "Animal life of north-east Scotland." Rep. British Ass. (Appendix): 20–6.

Describes the changes in fauna from glacial times to the present day in Scotland, with references to introduction and extinctions.

108. Wiesner, B. P. & Sheard, N. M. (1935). "The duration of life in an albino rat population." Proc. Roy. Soc. Edinburgh, 55: 1–26.

Under observation conditions 30 % of a Wistar rat population died from various causes before reaching the age of 30 days; the mean duration of life of the females was 693·1 days, and of males 669·37 days. Life tables.

109. Tucker, B. W. (1935). "The rookeries of Somerset." Proc. Somersetshire Archaeol. and Nat. Hist. Soc. 81: 149–240.

A detailed account of the distribution of 35,643 rook nests investigated by local ornithologists and Boy Scouts. 669 rookeries are described in tabular form; the type of site, number of nests, and species of trees are listed. 30 recorded species of trees were observed with nests; of these 93 % of the total number were elm, oak, beech, Scots pine, and ash; of these elm constituted about 50 %. The average size of a rookery was 53·4 nests; number of nests per sq. mile: 21·8.

110. Hollom, P. A. D. (1936). "Report on great crested grebe sample count, 1935." British Birds, 30: 138–58.

Counts made by many observers covering nearly half of Britain, for comparison with absolute count in 1931. A gross increase of 3 % is recorded, but 6 % fewer breeding pairs. Thames Valley area and most reservoirs showed decrease owing to drought years 1933 and 1934.

111. Venables, L. S. V. & Lack, D. (1936). "Further notes on territory in the great crested grebe." British Birds, 30: 60–9.

Detailed observation at Frensham Ponds, Surrey. Most individuals showed no territorial aggression. Territory concerned only with nesting site and not considered important for this species.

112. Nicholson, E. M. (1936). "The index of heron population, 1936." British Birds, 30: 202–5.

Slight increase in Britain. Data on local movements and changing numbers in heronries.

113. Boyd, A. W. (1936). "Report on the swallow enquiry, 1935." British Birds, 30: 98–116.

Detailed records from 23 areas in British Isles. First broods are largest. Swallows lay more eggs in north than in south of Britain. Census on 11 sample areas showed average density of 9 pairs per 1000 acres. Contains records of parasites and other animals found in nests, and notes on house martins.

114. Williams, T. S. (1936). "Bird life round Formby. Past and present distribution of the mistle-thrush." Northw. Nat. 11: 122–5.

The mistle-thrush is increasing in this district, where farm enclosures and game sanctuaries act as checks to natural enemies.

115. Hamilton, D. (1935). "Increase of the lesser redpoll as a breeding species in the Lothians." Scottish Nat. 121–3.

116. Clancey, P. A. (1935). "Increase and decrease of certain birds in East Renfrewshire and West Lanarkshire." Scottish Nat. 171–2.

Increase in 1934–5 of magpie, lesser redpoll, yellow wagtail, long-tailed tit, great spotted woodpecker, and barn owl. Decrease in sandpiper and sand-martin. No actual counts are given.

117. Charteris, G. (1936). "Proportion of sexes in roosting chaffinches." British Birds, 30: 117–19.

Large numbers netted at night. Males constantly dominant (64 %) in four areas but females 53 % in another.

118. Lucas, C. E. & Henderson, G. T. D. (1936). "On the association of jelly-fish and other organisms with catches of herring." J. Mar. Biol. Ass. U.K. 21: 293–304.

An interesting beginning in the application of simplified "questionnaire methods" to marine biological problems. 114 observations were supplied by skippers at the time of shooting their gear. From a comparison of these catches with the weekly port averages a negative relation was demonstrated between herring and small jelly-fish, white ones in particular.

119. Hardy, A. C., Lucas, C. E., Henderson, G. T. D., & Fraser, J. H. (1936). "The ecological relations between the herring and the plankton investigated with the plankton indicator. Parts I–IV." J. Mar. Biol. Ass. U.K. 21: 147–291.

An improved indicator is described. These instruments are towed behind a drifter at 7–10 fathoms for 1 mile before nets are shot. A series of such samples is arranged in ascending order of *Calanus* densities and the average herring catch associated with the upper and lower halves of the series is reckoned. The total catch that would have been made if fishing in the *Calanus*-poor waters had been at the same rate as in the rich is expressed as percentage theoretical gain or loss on the actual total. It is shown that a skipper consistently avoiding *Calanus*-poor waters would stand to make larger catches (Shields fishery, 1932–3: 21·2 ±7·5 %; Scottish fishery, 1931–3: 24·5 ± 7·7 %). The *Calanus*-herring correlation fluctuates seasonally. A tendency is shown for herring to avoid large quantities of *Limacina*. A standard and a miniature indicator were used for locating phytoplankton patches. There was a general negative correlation of these with herring; also with both *Calanus* and *Limacina*. The indicator may be used commercially for the avoidance of unsuitable waters.

120. Raitt, D. S. (1936). "The haddock stocks of the north-east Atlantic, 1916–1935." Fisheries, Scotland, Sci. Invest., 1936, No. 1: 1–32. (Edinburgh: H.M. Stationery Office. Price 1*s.* 6*d.*)

Haddock seldom occur in waters over 200 m. deep. Their further intolerance of salinities and temperatures outside narrow limits maintains the geographical distinction of several stocks. The value of the world haddock fishery is some 4½ million pounds per annum. For the North Sea numerical values are assigned for the first year strength of each year-class. Available observations on the strength of broods of other stocks are presented, together with a good summary of Russian work. From these data the broods are classified into successful (+), unsuccessful (−) or intermediate (I). It is found that fluctuations in the success of the broods fully support the conception of geographical isolation of the different stocks. Thus in the North Sea (1916–34) there were: 6 + and 7 − broods to 7 + and 3 − at Iceland with no general coincidence of +, − or I years at either place. Similarly it is concluded that the replenishment of all the main stocks goes on independently in time and extent. Thus it is hoped an annual forecast will some day be made of those stocks which may most profitably be exploited in following seasons.

121. Davis, F. M. (1937). "An account of the fishing gear of England and Wales. Third Edition (Revised, 1936)." Ministry Agr. Fish., Fish. Invest. Ser. 2, 15, No. 2: 1–139. (London: H.M. Stationery Office. Price 6*s.*)

A complete and interesting account well illustrated. Describes the history of different methods, making and mending nets, and types of gear from trawls to lobster pots. There is a chapter on sparing of undersized fish, and a useful selected bibliography of 129 references.

122. Clapham, A. R. (1936). "Over-dispersion in grassland communities and use of statistical methods in plant ecology." J. Ecol. 24: 232–51.

These methods of analysis are useful also for animal population studies.

123. Carpenter, J. R. & Ford, J. (1936). "The use of sweep net samples in an ecological survey." J. Soc. Brit. Ent. 1: 155–61.

The value of sweep net samples is discussed and the results of a number of sweepings of different sizes taken at the same time for two habitats. By statistical analysis it is shown that the most reliable number of sweeps to obtain a representative sample in a grass community is 75, and for a rosette-plant community 100. Personal error is important and varies from day to day. Dispersal varies according to weather and habitat. The method is recommended as simple, rapid and fairly efficient.

124. Milne, P. S. (1936). "A device for the rapid counting of large numbers of small insects." Bull. Ent. Res. 27: 269–71.

The apparatus provides for transference to a turntable, examination with a binocular and removal by suction.

125. Ladell, W. R. S. (1936). "A new apparatus for separating insects and other Arthropods from the soil." Ann. Appl. Biol. 23: 862–79.

The principle of flotation is used. From fallow land 60·6 million animals per acre were recorded and from new grass land 121·4 million per acre. These are high figures when compared with other methods.

126. MacLagan, D. S. (1932). "The effect of population density upon rate of reproduction with special reference to insects." Proc. Roy. Soc. B, 111: 437–54.

Populations of flour beetles, *Tribolium confusum*, have an optimum density at which rate of reproduction is greatest. Grain weevils, *Sitophilus granarius*, show a hyperbolic relationship between population density and progeny per weevil, the latter decreasing at successively higher densities. Repeated contacts at high densities interfere with oviposition. Another factor is the utilization of grains for egg-laying. Maximum oviposition and maximum utilization of grains do not occur at the same density. Presence of the moth *Sitotroga cerealella* lowers the rate of reproduction, but not so much as would the addition of an equal number of weevils.

127. MacLagan, D. S. & Dunn, E. (1936). "The experimental analysis of the growth of an insect population." Proc. Roy. Soc. Edinb. 55: 126–39.

In populations of the grain weevil *Sitophilus oryzae* there is an optimum density for frequency of copulation. This is another factor contributing to the formation of an optimum density for rate of reproduction. Oviposition bears the same relation to density as in populations of *S. granarius*.

128. Evans, A. C. (1936). "A note on the hibernation of *Micraspis sedecimpunctata* L. (var. 12-*punctata* L.), (Col. Coec.), at Rothamsted Experimental Station." Proc. R. Ent. Soc. Lond. A, 11: 116–19.

An aggregation of this species of ladybird hibernating on a gate-post numbered, on the south face, 3000–4000; on the east, 120; on the north, 265; on the west, 200. Many thousands were present in the surrounding grass. The prevailing winds were between N.E. and N.W. The aggregation was formed at the end of October and increased in size for about a fortnight. The beetles collected into variously sized groups, initiated by obstacles or crevices in their path as they crept upwards. Females were less abundant than males, their ovaries were undeveloped. Hibernation did not consist of complete dormancy, for under favourable conditions they climbed upwards, and during inclement weather they apparently dropped to the ground. By the end of April the numbers on the post were greatly reduced and complete dispersion took place on 6 May.

129. H[arrison], J. W. H. (1936). "The occurrence of certain resident butterflies in the Team Valley." Vasculum, 22: 112.

Epinephele jurtina has regained and held all the ground lost in the first decade of the century.

130. Laidlaw, W. B. R. (1936). "The brown lacewing flies (Hemerobiidae): their importance as controls of *Adelges cooleyi* Gillette." Ent. Mon. Mag. 72: 164–74.

It is calculated that two parent *Hemerobius stigma* and their offspring will in one year devour approximately 4 million *Adelges*.

131. Donisthorpe, H. (1936). "*Cathartus* (*Ahasverus*) *advena* Waltl in the open." Ent. Mon. Mag. 72: 228.

Tens of thousands of this beetle at the bottom of a haystack.

132. Glasgow, J. P. (1936). "The bionomics of *Hydropsyche colonica* McL. and *H. philpotti* Till. (Trichoptera)." Proc. R. Ent. Soc. Lond. A, 11: 122–8.

Gives a table of the fauna of one sq. yd. of each of two New Zealand streams.

133. Brown, J. M. (1936). "Collembola swarms." Naturalist: 252.

Sminthurinus aureus swarming on top of wall, October.

134. Gibbons, S. G. (1936). "*Calanus finmarchicus* and other Copepods in Scottish waters in 1933." Fisheries, Scotland, Sci. Invest., 1936, No. 2: 1–37. (Edinburgh: H.M. Stationery Office. Price 2*s*.)

Extensive sampling as part of a plan ultimately to predict plankton movements and the dependent feeding of herring shoals. *Calanus* were more abundant at the surface by night than by day. This difference in catch increased with length of night, indicating maximum vertical diurnal migration in winter. The horizontal distribution from Feb.–Nov. is given. For the year as a whole the top and mid-waters were richer north of 57° 30′ N. than to the south; the bottom populations were about the same. In the north, 38–43 % were mature; in the south 53–60 %. This is consistent with a northern influx of upper water bearing chiefly adolescent forms. In the North Sea the modal lengths of adult females were March: 2·7–2·9 mm.; May: 3·4 mm. The origin of the later stock is a problem of some complexity as, though 93 % mature, the March population consists of only 3·35 % males. The ratios of eggs to nauplii and nauplii to copepodid stages are much greater than unity in Feb.–Mar. and indicate some breeding on the part of the winter carry-over stock. Later on the ratios fall to much less than unity and indicate an influx with the currents from north and west. The relative importance of carry-over and influx populations is being investigated.

135. Fox, H. M. & Newth, H. G. (1936). "On the swarming of *Vorticella*." Proc. Zool. Soc. Lond. 309–13.

Vorticella campanula and *V. chlorostigma* form periodic swarms, held together by mucous threads. Apparently independent of asexual reproduction and conjugation.

7. MIGRATION, DISPERSAL, AND INTRODUCTIONS

See also **72, 89, 134**

136. Vesey-Fitzgerald, B. (1936). "Welcome or unwelcome guest?" The Field: 1075.

Spread of Continental dormouse (*Glis glis*) from centre of introduction at Tring.

137. Anon. (1936). "Recovery of marked birds." British Birds, 30: 74–9, 125–30; and (**1937**), 30: 254–8.

Detailed records of recoveries of birds ringed in British Isles.

138. Midlothian Ornithological Club (1935). "Isle of May Bird Observatory. Report. Spring, 30th March to 2nd June 1935." Scottish Nat.: 125–34.

A trapping station has been set up for catching and ringing birds. The 1935 spring migration dates were abnormal for a number of species. Detailed records are given of birds seen on the island, and the total number of each species (altogether 245 adults, 163 nestlings) ringed.

139. Bryant, C. H. (1936). "Return migration of jays." British Birds, 30: 80.

Movements south-westerly in autumn and easterly in spring, in Sussex.

140. Mackworth-Praed, C. W. & Gilbert, H. A. (1936). "Further notes on Orielton decoy, 1935–36." British Birds, 30: 159–61.

Number of duck, etc. caught, with record of sexes. Map showing movements of teal after ringing.

141. Wild, S. V. (1936). "The vicissitudes of a small rookery." Northw. Nat. 11: 8–17.

Observations in Cheshire made over a period of 8 years. Possible causes of dispersal and desertion are reviewed. It is suggested that a parent rookery may give rise to several smaller ones.

142. Anon. (1936). "Unusual numbers of little stints." British Birds, 30: 195 and 230.

Records from many parts of Britain, autumn 1936.

143. Booth, H. B. (1936). "Fulmar petrels nesting on the Farne Islands." Naturalist: 199.

5 or 6 pairs in June 1936.

144. Nall, G. H. (1936). "Notes on sea-trout from the Dee tidal nets, Aberdeen, 1935." Fisheries, Scotland, Salmon Fish., 1936. No. 4: 1–22. (Edinburgh: H.M. Stationery Office. Price 1*s.* 6*d.*)

The population is composed of fish from many other waters and a wide range of growth rate is shown. There is no evidence of a spring run. An unusually large proportion of the sample (83·7 %) were maiden fish, average weight 1 lb. 11 oz. The lengths of smolts at migration are similar to those of the two Esks and the Montrose coast.

145. Lloyd, Ll. & Turner, J. N. (1936). "The migrations of the larvae of *Metriocnemus longitarsus*, Goet. (Chironomidae) in response to gravity and light." Proc. Leeds Phil. Lit. Soc. 3: 177–88.

Experiments show that phototropism is intensified with decreased O_2 concentration, as are geotropic responses. Below 16° C. larvae are much less active than above that point. Food selection and natural breeding places are also discussed. Migration to near the surface before pupation is attributed to physiological change.

146. Thomas, I. (1936). "On the occurrence in England of the pear fruit saw-fly, *Hoplocampa brevis* Klug." Ann. Appl. Biol. 23: 633–9.

This Continental pest is now recorded as an English one. A preliminary study of the biology.

147. Fletcher, T. B. (1936). "Marked migrant butterflies." Ent. Rec. 48: 105–6.

A small patch on the upper surface of the right forewing is rubbed clear of scales and a small label, written in Indian ink on tracing paper, is attached to it with Canada balsam; the adhesive is allowed to harden and the butterfly then released. Of 75 individuals thus marked only 3 remained in the vicinity for any appreciable period.

148. Dannreuther, T. (1936). "Migration Records, 1936." Entomologist, 69: 154–6, 182–6, 225–30, 255–9.

Records early in 1936 were rather scarce perhaps owing to cold weather on the Continent. Considerable immigration of *Plusia gamma* associated with *Nomophila noctuella* and *Vanessa cardui* in latter half of June. *Plusia gamma* crossing the English Channel in opposite directions on successive nights at points 200 miles apart, into Hastings and south-by-west from the Start and Gloucestershire. Partial autumn emigration confirmed.

149. Garrett, F. C. (1936). "Migrant Lepidoptera in 1936." Vasculum, 22: 97–8.

Few records were received in the north of England in 1936; *Plusia gamma* alone was common. See also 1936, Vasculum, 22: 149, 152, 154, 155.

150. Pitman, C. M. R. (1936). "An observed immigration of butterflies at Studland Bay, Dorset." Entomologist, 69: 168–9.

Colias croceus, Pieris rapae, Vanessa cardui, Vanessa atalanta and *Aglais urticae* coming in from the sea on 5 September.

151. Allan, P. B. M. (1936). "Some notes on collecting Lepidoptera in the Bishop's Stortford district in 1936." Ent. Rec. 48: 119–21.

The migrant moth *Agrotis ravida* occurred in numbers. The butterfly painted lady (*Polygonia c-album*) has established itself in the district.

152. Andrewes, H. L. (1936). "Early records of *Vanessa atalanta* L. (Lep.)." J. Soc. Brit. Ent. 1: 162.

Records of this butterfly on the wing in February, March and April support the view that it hibernates in England.

153. Tomlin, J. R. LeB. (1936). "*Macroglossum stellatarum* at Hastings." Entomologist, 69: 208.

Unusual concentration of hundreds on 24 June.

154. Clarke, W. J. (1936). "Immigration of silver Y moths at Scarborough." Naturalist: 252.

Large numbers present for short time at end of Aug. 1936.

155. Wheeler, G. (1936). "Immigration of *Plusia gamma*." Ent. Rec. 48: 102–3.

Large numbers of this moth observed at Worthing, 23 Aug. 1936; ten days later they seemed to have disappeared.

156. Anon. (1936). "Notes on some interesting animals stranded on the west coast of Scotland during the summer of 1935." Scottish Nat.: 27–8.

Includes signed notes by **J. B. Beatson, E. A. T. Nicol,** and **C. Elton.** These record the occurrence of the floating Mollusc, *Ianthina britannica*; the siphonophore, *Velella spirans*; and the barnacle *Lepas fascicularis*. These are all southern forms not usually met with in British waters; they indicate a strong flow of southern Atlantic water to Scotland in 1935.

BRITISH ECOLOGICAL SOCIETY

SUMMER MEETING IN SOUTH-WEST IRELAND, 12–21 AUGUST 1936

FOLLOWING the kind invitation of Prof. Renouf, and the promise of active assistance by Dr Lloyd Praeger, the summer excursion was held in south-west Ireland, beginning at Cork, taking in the Biological Station at Lough Ine and finishing at Killarney. The local organization was in the hands of Prof. Renouf and Dr Praeger.

12 *August.* The party was met in Cork by Dr and Mrs Praeger and travelled by bus to Skibbereen. The afternoon was spent at Baltimore, where the rocky headlands are covered by a low-growing *Ulex gallii* heath with *Erica cinerea* abundant. A small pond in this region showed an interesting zonation; the centre was colonized by *Sparganium minimum* and at the water margin there was a fringe of *Glyceria fluitans* and *Apium inundatum*. Outside this was a belt 2–5 ft. wide of *Galium palustre* and *Hypericum elodes*, together forming a thick mat. Beyond this the heath vegetation began, but near the pond there was mixed with it an abundance of *Juncus acutiflorus*. In another small boggy hollow various marsh species were found, such as *Scutellaria minor*, *Anagallis tenella*, *Orchis maculata*, *Lythrum salicaria* and Sphagna.

In the evening Prof. Renouf and Dr Praeger gave short talks concerning the district and the proposed expeditions. Dr Praeger described the geology of south-west Ireland and said that bands of slate and limestone alternate, running in an east-west direction. The limestone has nearly all weathered away, leaving valleys which have cut across the main north-south drainage direction; the latter is only apparent at the mouths of the rivers, which open to the south coast.

13 *August.* A visit was paid to the valley which opens to the coast at Trealispean, where there is an interesting series of plant communities passing from a freshwater fen down to maritime types. The former showed a very irregular surface, suggesting human interference, with occasional patches of *Cladium Mariscus*, and bushes of *Salix cinerea* and hybrids. *Osmunda regalis* was common in this type of community both here and elsewhere. The remaining vegetation contained many fen species, e.g. *Lythrum salicaria*, with *Juncus acutiflorus* as the commonest. *Sphagnum cymbifolium* and *S. plumulosum*, however, were also fairly abundant. Lower down the stream the valley widened out and was filled by a dense Phragmitetum containing *Angelica sylvestris*, *Carex paniculata*, etc. and much resembling the Broads vegetation. Farther on *Phragmites* was still dominant but the fen species had disappeared, giving place to species characteristic of brackish or salt water, e.g. *Atriplex* and *Spergularia* spp. At the mouth of the stream was a grey dune bearing large patches of *Juncus acutus*, and, on the seaward side, much scattered *Eryngium maritimum*.

14 *August.* Prof. Renouf very kindly invited the members of the party to spend the day at the Marine Biological Laboratory at Lough Ine. As it was low tide when they arrived it was possible to examine the sheltered corner, where a small saltmarsh has developed. The lower-lying mud was thickly covered by *Zostera nana* and *Enteromorpha* spp., while rising out of it were level areas up to 30 ft. across with vertical sides, at about 1 ft. higher than the Zosteretum: these bore *Juncus maritimus*, *Phragmites*, and very large tufts of *Plantago maritima*. A sea meadow of *Glyceria maritima* and *Salicornia* occupied the ground just behind a slight sea wall. The algal zonation was clearly seen at low tide in the rapids between the Lough and the sea.

The afternoon was spent in short boat trips in search of algae and in examining the very interesting exhibits in the laboratory. Prof. Renouf showed some of the marine fauna

including a number of sponges. Among the latter were *Hymeniacidon caruncula, Sarcodictyon catenata, Tethya lincurium* (producing buds), *Terpios fugax, Leucoselenia coriacea* (with coloured metamps) and *Pachymatisma Johnstoni* (showing colour variation according to light intensity). Other species shown were *Parethropodium hibernicum, Caryophyllia Smithii, Marthasterias glacialis, Descitus Bucklandi, Clione celata,* and *Halicondria panicea.* A large number of Lichens were shown by Mrs Porter, illustrating the lichen flora of different types of habitat. The members of the expedition were very much indebted to Prof. and Mrs Renouf and other friends and workers at Lough Ine for their generous hospitality and for a day of much scientific value and enjoyment.

15 *August.* The party left Skibbereen by bus for Glengariff, travelling through Drumoleague and Dunmanay. The country became more hilly and the dry gorse heath gave place to upland bog vegetation. Afforestation experiments could be seen on the way; these are still in the earliest stages. Much peat-digging goes on here but the peat is so full of birch remains that it has to be worked by hand. Two hours were spent at Gougane Barra, a mountainous valley opening into a small lake. The latter, like others in this region, was fringed with *Nymphaea* (*Castalia*) *alba* and *Phragmites.* The hillside and valley vegetation was mainly of the *Molinia-Calluna-Erica* type to be described later. In the valley bottom there were well-marked drainage channels, most of them artificial, with an abundance of Sphagna, especially *S. cuspidatum* var. *submersum. Potamogeton natans, Hypericum elodes* and *Viola palustris* were common.

16 *August.* The day was spent in examining the exotic species cultivated in the gardens of Glengariff and Illaungariff Island. Among the plants seen were *Eucalyptus globulus, Crinodendron Hookeri, Diarenia* (*Spiraxis*) *pulcherrima, Olearia semidentata, Callistemon lanceolata, Epacris longiflora, Dabeocia cantabrica* and *Erica Mackaiana* (the last two native to west Ireland); and species of *Leptospermum, Acacia, Melaleuca* and *Lomatia.*

17 *August.* The *Quercus sessiliflora* woods[1] which are a feature of south-west Ireland are represented both at Glengariff and at Killarney and were studied by the party in both places. The woods give the impression of an almost pure oak canopy with a shrub layer of holly and a most strikingly luxuriant development of the moss flora. The woods for the most part occupy the lower hill slopes on which boulders are very numerous, and these boulders and the oak trunks generally carry thick cushions of Bryophytes and species of *Hymenophyllum.* The epiphytic flora is more abundant than that in English oakwoods, *Polypodium vulgare* being the commonest epiphyte.

The other frequent trees are *Sorbus aucuparia, Betula pubescens, Fraxinus excelsior,* and *Fagus sylvatica,* the last said always to be planted. *Arbutus unedo* is found marginally and in scrub associations. In the neighbourhood of parks and gardens subspontaneous *Rhododendron ponticum* has taken the place of *Ilex* in the shrub layer, and appears to be spreading successfully, as seedlings are abundant. It is possible to find seedlings of all the trees mentioned, but those of *Sorbus aucuparia* and *Ilex* are the commonest.

The following list includes the more abundant species of the ground flora:

Vaccinium myrtillus	Lastraea aemula	Hylocomium loreum
Luzula maxima	Euphorbia hiberna	H. brevirostre
Blechnum spicant	Agrostis vulgaris	Thuidium tamariscinum
Oxalis acetosella	Lonicera periclymenum	Plagiothecium undulatum
Pteridium aquilinum	Hedera helix	Plagiochila denticulata
Calluna vulgaris	Hymenophyllum tunbridgense	Scapania dentata
Potentilla erecta	H. unilaterale	Diplophyllum albicans

There is much variation in the size of the oak trees from place to place, and where they are smaller there is no clear distinction into tree and shrub layers, for the hollies may be as tall as the oaks. This modification of the canopy is probably responsible to a large extent

[1] Cf. **Rübel, E.** "The Killarney Woods," *New Phytol.* **11**, pp. 54–7, 1912.

for the variations in relative abundance and luxuriance of the characteristic species of the ground flora. On some of the hill slopes in the Killarney region there appears a fairly well-defined altitudinal limit to the woods, and on the whole *Betula* becomes more abundant at the upper margin. It is not, however, possible to be sure that this tree-limit is a genuine expression of climatic conditions without some knowledge of the relation of elevation and aspect to the development of this type of wood, and at present there are but few data on this subject. Among the other ecological factors which probably influence the distribution of woodland one may mention drainage and grazing by animals. On flat boggy sections of the course of a stream there usually develops a *Molinia* meadow with very tall tussocks of the grass. Birches and occasionally alders may be found in such places, but not oaks or hollies. Dead hollies, however, occur frequently here and also on the margins of the wood, and this is often due to destruction of the bark by deer or goats. Rabbits are scarce in this part of the country, but deer are numerous and quite possibly their grazing has an effect on the regeneration of woodland. Soil differences very likely affect the growth of the oaks and thus produce the various facies that are shown by the woods as a whole, but this question is at present under investigation by members of the Cambridge Botany School.

18 *August.* The party travelled to Killarney by bus via Kenmare.

19 *August.* The woods around the upper lake of Killarney were visited.

20 *August.* Some members of the expedition visited Ross Island and examined the oakwoods developed on the limestone. Besides the native plants of interest, including several species of *Sorbus*, there were a number of introductions from subtropical regions. The other members spent the day on the slopes of Carrantouil, ascending via the Hag's glen. From observations made in this region, at Gougane Barra, and on Sugarloaf Mount and in the neighbourhood of Barley Lake near Glengariff, one may roughly divide the upland vegetation of this part of Ireland into four types.

(1) *Molinia-Calluna-Erica cinerea* bog. This community was well shown at Gougane Barra, and is characteristic of much of the lower hillsides, especially where the ground is sloping. The *Molinia* forms tussocks to some extent, and with the scattered bushes of *Calluna* and *Erica* makes the surface uneven. Sphagna are abundant, particularly *Sphagnum cymbifolium*, *S. rubellum*, and *S. plumulosum*. *Myrica gale* is nearly always present, while on ridges and relatively dry ground *Ulex gallii* and *Pteridium* are common. *Narthecium ossifragum*, *Rhynchospora alba* and *Drosera rotundifolia* are abundant, with *Scirpus caespitosus*, *Eriophorum vaginatum*, and *E. angustifolium* rather less frequent.

(2) *Rhynchospora-Molinia* bog. This contains the same species as the first type, but showing different growth forms and relative abundance. It develops characteristically on flatter surfaces, whether these are on high mountain shoulders or in valley bottoms. The following are the main components:

Rhynchospora alba	Eriophorum vaginatum	Erica tetralix
Molinia coerulea	Calluna vulgaris	Sphagna
Narthecium ossifragum		

These form a vegetation with a fairly even surface because the *Molinia* has a stoloniferous habit and the *Calluna* is very inconspicuous as a rule, being sometimes only 2 in. high. *Scirpus caespitosus* and *Schoenus nigricans* are locally abundant. There are, however, several different facies included in this general heading:

(*a*) *Eriophorum vaginatum* may be sufficiently abundant to give a true cotton-grass moor; in this peat erosion may often be seen, as for example in the Hag's Glen, where tree stumps are exposed, and the bare pavement is being colonized by *Juncus squarrosus*, *Calluna*, *Polytrichum* spp., etc.

(*b*) In the hollows left by peat-cuttings in the valleys *Rhynchospora* is very abundant, and where there is an inch or two of standing water, *Eriophorum angustifolium* forms almost pure

stands. At a slightly later stage, *Molinia* comes in with the Sphagna, *Narthecium*, etc. and then invasion by *Myrica* seems to follow almost invariably.

(*c*) In undisturbed valley bottoms with a considerable area of flat ground, numerous small pools are scattered through the vegetation and Sphagna appear more active, giving something of the nature of the "regeneration complex" of raised bogs. In some the general physiography is also of the raised bog type. The pool Sphagna are *S. cuspidatum* and another species, while the tussock builders are first *S. magellanicum*, frequently accompanied by *Campylopus atrovirens*, then various other Sphagna such as *S. rubellum* and *S. plumulosum*. *Rhacomitrium lanuginosum* is perhaps the commonest constituent of the tussock tops. The latter are, however, very inconspicuous and almost always bear *Molinia* in a somewhat tufted condition; though *Calluna* and *Erica tetralix* occur frequently they are not conspicuous and *Cladonia sylvatica* never develops extensively. *Narthecium* and all three species of *Drosera* are widespread. *Myrica* is not found in this particular facies, though in one case where a bog of this type was well developed there was an obvious "rand", with no pools and with abundant *Myrica*.

(3) *Rhacomitrium* moor. On the higher mountain slopes, above about 2500 ft., there is a moorland type in which *Rhacomitrium* is very abundant though not dominant. The following list was made on the slopes of Carrantouil:

Rhacomitrium lanuginosum	Galium saxatile	Nardus stricta
Calluna vulgaris	Hylocomium loreum	Juncus squarrosus
Vaccinium Myrtillus	Luzula maxima	Rhacomitrium heterostichum
Potentilla erecta	Campylopus flexuosus	

Juncus squarrosus and *Calluna* seem to be complementary to one another and it is conceivable that these two are characteristic of different phases in cycles of slight local erosion, of which traces can be seen.

(4) *Arctic-alpine vegetation.* In the high gullies and steep scree slopes *Calluna* and *Erica* are scarce and *Molinia* not abundant; the grasses are mainly *Festuca ovina* and *Nardus stricta*. Bryophyta are abundant and include many of the typical mountain species such as *Herberta hutchinsiae*, *Scapania ornithopodioides*, *Pleurozia purpurea* and a rarer species of *Leptodontium*. An interesting plant found in the Hag's Glen was the naturalized New Zealand species, *Epilobium nummulariifolium*.

On the last evening Prof. Osborn and Dr Turrill spoke on behalf of the members of the expedition and of the British Ecological Society as a whole. They expressed most cordial thanks to Dr and Mrs Praeger for the great kindness they had shown throughout the expedition, which was felt by everyone to have been exceedingly interesting and enjoyable.

VERONA M. CONWAY.

ANNUAL MEETING AT UNIVERSITY COLLEGE, LONDON
8–9 JANUARY 1937

SOIRÉE IN THE DEPARTMENT OF BOTANY

ON the evening of Friday, 8 January, about ninety members and guests were entertained at a soirée in the Department of Botany, University College.

A series of interesting exhibits was shown. Mr D. Chitty demonstrated a ringing technique for small mammals, and types of traps with nesting boxes and observation lids. He exhibited a map of Bagley Wood, near Oxford, showing results of studies there upon the movements of the wood-mouse (*Apodemus sylvaticus*) and *Clethrionomys* (= *Erotomys*) the bank vole. The wood-mouse is much the more active, sometimes travelling as much as

150-200 yards in two nights. Prof. Salisbury had set out specimens and drawings to show the root systems of some twenty-two species of dune annuals. He also showed samples of dune sand of increasing ages from the Portuguese coast and from Southport. Analyses showed progressive leaching of carbonates and accumulation of organic matter: there was also shown a series of dwarf ecads of *Desmazeria loliacea*. Mr K. Wilson demonstrated an ingenious potometer for use with aquatic plants. It depends upon separate measurement of gas evolved from the cut stem and of the total volume change in the water reservoir. The apparatus is very compact, and is designed to avoid pressure and distance errors during manipulation. Dr V. J. Chapman showed sections of salt-marsh deposits from the east coast of North America, including a "marine peat" rich in silt, which had formed above a fresh-water marsh at Scituate, after a storm breach made in 1898. The "marine peat" is already several inches thick. Results were also given for sand strip marking in measuring the rates of accretion of salt marsh deposits. Dr F. W. Jane showed a large number of drawings, microscopic drawings and descriptions of rare or unrecorded green algae and flagellates, including what may prove to be new species of *Chlamydomonas* and *Cyclonexis*. It may well be that some of these forms are not uncommon, but have not been looked for. Mr D. Coult had working an apparatus for investigating the effects of shaking on plants. With *Sinapis alba* it has proved possible to show that both slow and fast shaking increases germination rate by a statistically significant amount.

THE ANNUAL MEETING

The twenty-third Annual Meeting of the Society was held in the Department of Botany, University College, London, on the following morning, Saturday, 9 January, at 10.30 a.m., the President, Dr W. H. Pearsall, occupying the chair. The minutes of the previous meeting were read and confirmed. The report of the Honorary Secretary was then read and adopted.

Hon. Secretary's Report for the year 1936

The twenty-second annual meeting of the Society was held in the Department of Botany of the University of Reading, on 3, 4 and 5 January. On the first day papers were read in the afternoon, and members inspected a series of exhibits in the botanical laboratories. In the evening a soirée was held in Wantage Hall at which about fifty members and guests were present. The meeting was resumed with a large attendance on the following morning, and closed in the afternoon. On the morning of the 5th there was a short excursion to the heath and woodlands near Peppard Common. The Society owes very hearty thanks to Prof. and Mrs Harris and to the University authorities who so kindly and ably entertained us.

The summer excursion of the Society was held in south-west Ireland from 12 to 21 August. It was under the leadership of Dr Lloyd Praeger and Prof. Renouf, and the Society is most grateful to them and to Mrs Praeger for the trouble they took in arranging the meeting and conducting the party of eighteen over exceptionally interesting ecological ground.

The autumn excursion with the British Mycological Society was held at Ranmore Common near Dorking (Surrey) under the leadership of Mr J. Ramsbottom. The day was fine and the attendance large.

In the past year two numbers of vol. v of *The Journal of Animal Ecology* have been published, appearing in May and November. They contained respectively 230 and 186 pages, representing a further advance in size over previous volumes. In all twenty-four original papers were published, with 10 plates, in addition to notes, notices and reviews. Notices of publications on Animal Ecology in this volume totalled 276.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1936

Income

	£	s.	d.	£	s.	d.
Subscriptions received, including arrears	481	17	5			
Less Prepayments for 1937–9	16	0	0			
	465	17	5			
Less Transferred to *Journal of Animal Ecology* (see below)	181	7	6			
				284	9	11
Interest on Investments	34	10	0			
Interest on Deposit Account		13	7			
				35	3	7
Journal of Ecology—Sales, etc.:						
Current volume, XXIV, 1936	479	14	3			
Back volumes and parts	27	5	8			
Sales of reprints	39	0	5			
Advertising space	3	13	6			
				540	13	10
Index volume, *Journal of Ecology* (vols. I–XX), Sales				3	1	8
Journal of Animal Ecology—Sales, etc.:						
Vol. v, 1936: Subscriptions received (see above)	181	7	6			
Sales	197	4	1			
Sales of reprints	76	16	3			
Vols. I–IV: Sales of back numbers	52	6	7			
				507	14	5
				£1371	3	5

Expenditure

	£	s.	d.	£	s.	d.
Working Expenses:						
Printing Circulars, etc.	5	10	6			
Postages	8	17	7			
Bank Charges		7	2			
Clerical assistance (Secretary and Treasurer) ...	15	0	0			
				29	15	3
Audit Fee				3	3	0
Grants:						
Freshwater Biological Association of the British Empire	10	0	0			
B.E.S. Transplant Experiments Fund	5	0	0			
				15	0	0
Soirée Expenses				2	16	7
Journal of Ecology, vol. XXIV (1936):						
Paper, Printing, Illustrations, etc.	646	1	8			
Binding	2	1	0			
Carriage, Insurance, etc.	44	13	1			
Publishers' Commission	74	7	4			
				767	3	1
Index Volume, *Journal of Ecology*, vols. I–XX:						
Sundry Expenses				1	19	4
Journal of Animal Ecology, vol. V (1936):						
Paper, Printing, Illustrations, etc.	479	7	2			
Carriage, Insurance, Advertising, etc.	30	8	2			
Publishers' Commission	41	0	1			
				550	15	5
				1370	12	8
Balance, Surplus for the Year					10	9
				£1371	3	5

BALANCE SHEET AT 31 DECEMBER 1936

Liabilities

	£	s.	d.	£	s.	d.
Membership Subscriptions, prepaid for 1937, etc. ...				16	0	0
Journal of Animal Ecology, vol. v, Part 2, 1936:						
Printing Account due	229	1	5			
Less Sale of reprints	27	7	0			
				201	14	5
Library Account				1	5	0
Journal of Ecology, 1937, Grant from University of London, carried forward				40	0	0
General Revenue Account, Balance of Funds:						
Balance at 31 December 1935	896	15	0			
Add Surplus for Year ending 31 December, 1936		10	9			
				897	5	9
				£1156	5	2

Assets

	£	s.	d.	£	s.	d.
Westminster Bank Ltd.—Credit Balances:						
Current Account	90	12	2			
Deposit Account	150	0	0			
				240	12	2
Investments:						
£700 3½% War Loan, at cost (Market value at 105½, £738. 10*s.*)	717	3	0			
£200 5% Conversion Loan at cost (Market value at 117⅜, £234. 15*s.*)	198	10	0			
				915	13	0
				£1156	5	2

Audited and found correct and as shown by the Account Books of the Society. The Bank Balances have been verified by Bank Certificates.

(Signed) WM NORMAN & SONS,
Chartered Accountants.

120, BISHOPSGATE, LONDON, E.C. 2.
15*th January* 1937.

NOTE. A further asset is the unsold stock of the *Journals* and Index Volumes held for the Society by the Publishers.

(Signed) HUGH BOYD WATT,
Hon. Treasurer

Since the last annual meeting there have been issued two numbers of vol. XXIV of *The Journal of Ecology*, appearing in February and August and containing respectively 316 and 198 pages, with twenty-three plates. In this volume have been published twenty original papers, besides book reviews and notices. The Council has decided that if the size and quality of the *Journal* is to be maintained it will be necessary to increase the price to non-members from 30*s.* to 35*s.* as from 1 January 1937 and notice of this has already been published.

The Society's transplant experiments at Potterne are continuing satisfactorily in the hands of Mr Marsden Jones and Dr Turrill.

Since the last annual meeting the membership of the Society has risen from 341 to 343: twenty members have resigned or have died, and twenty-two new members have been elected. Of the present membership list, 191 members receive *The Journal of Ecology* alone, 100 *The Journal of Animal Ecology* alone, 49 receive both *Journals*, and two neither.

We much regret to note the death of Dr Frank Cavers, first Secretary and Honorary Editor to the Society: his extraordinary industry and ability greatly helped the establishment and early growth of the Society.

In the early part of the year the Hon. Treasurer suggested to Council that a second cheque signatory should be appointed, and it was agreed that Prof. Salisbury take this position.

The Secretary announced the provisional decision of the Council to accept the President's kind invitation to hold the Summer meeting at Wray Castle, Windermere, in September.

It was proposed from the Chair and cordially agreed to by the meeting that the Honorary Secretary be thanked for his services during the past year.

The Honorary Treasurer made a provisional statement of the financial position of the Society, reporting that during the past year income and expenditure had practically balanced (see statement on opposite page). The sum of £60 specially voted by Council towards the cost of printing Prof. Boycott's important and exceptionally long paper in *The Journal of Animal Ecology* was able to be paid out of income. The improvement over the previous year's working was partly due to increased sales of the *Journals* to non-members. A very hearty vote of thanks to the Honorary Treasurer was proposed by Mr Charles Oldham and carried unanimously. It was proposed by Prof. Matthews and carried *nem. con.* that Messrs Wm Norman and Son be reappointed auditors to the Society for 1937. It was proposed from the Chair and carried *nem. con.* that a grant of £5 be authorized towards the expenses of the Transplant Experiments of the Society.

The meeting then proceeded to the election of Officers as follows:

Vice-President: Dr W. B. Turrill.

Council Members: Dr A. S. Watt and Dr E. Ashby (retiring Dr W. B. Turrill, Dr T. W. Woodhead and Dr R. Gurney).

Hon. Editor of The Journal of Ecology: Prof. A. G. Tansley.

Hon. Editor of The Journal of Animal Ecology: Mr C. S. Elton.

Hon. Secretary: Dr H. Godwin.

Dr Pearsall then gave his extremely interesting presidential address on "The Soil Complex in relation to Plant Communities".

After the adjournment for lunch Mr J. Ford read a paper on the composition of animal communities. In a critical survey of the bases of investigations into the nature of the animal community, he regarded the food-chain as too complex and proposed alternatively an enlargement and modification of Elton's "Pyramid of Numbers". He showed the results of estimating the relative frequencies of different components of the animal populations of *Bromus erectus* grassland near Oxford. He put forward the concept of subordinate groupings within which one species might be substituted for another without affecting the unity of the community. Questions were asked by Prof. Boycott and Mr Elton.

Mr R. D. Misra gave an account of his investigations of the lake muds of the English Lake District. With progressive shallowing which accompanies the hydroseral sequence there is increasing organic content of the lake mud, and falling *p*H. The muds become strongly reducing, nitrogen exists as ammonia, sulphur as hydrogen sulphide and carbon as methane. Iron is in the ferrous state. Analyses of plant nitrogen and of the mud on which the plants grew strongly suggested that these rooted aquatics were very dependent on the nutritive content of the substratum. The President, Dr A. S. Watt and Dr Godwin took part in the discussion which followed.

Mr R. N. Robertson then gave an account of the vegetation region of eastern Australia, investigated by Prof. Osborn and himself. The Myall Lakes have been cut off by coastal sand-bars but are still drained by the River Myall. A full succession is recognizable from open water through reed swamp and *Melaleuca* swamp forest to *Eucalyptus robusta* forest. The tuff soil of the major part of the region is heavily podsolized and bears eucalypt forest with many different dominants. In patches and gulleys in the eucalypt forest are areas of broad-leaved sub-tropical rain-forest, cool and shady and with palms. The following discussion turned on the factors possibly involved in the distribution of the two woodland types, and Dr Burtt Davy, Dr Paul Richards and Dr Chapman took part.

Dr John Turner followed with an account of the results obtained by a Cambridge group of ecologists during an investigation of the *Quercus sessiliflora* woods of Killarney, south-west Ireland. The woodlands were divided into types which measurement showed to differ greatly in composition. Type 1 had tall oaks (70 ft.) widely spaced, with dense *Ilex* undergrowth, very dense shade, and ground flora poor both in individuals and species excepting Bryophyta. Type 2 had less tall (50 ft.) but more numerous oaks, often of pioneer form, sparser holly, a few other tree species and richer undergrowth. Type 3 was oak scrub up to 25 ft. tall, with holly, *Sorbus aucuparia*, birch, and ground vegetation rich in species and including tall flowering *Calluna* and *Vaccinium*. These types were considered to be determined by soil differences due to alternating bands of shale and sandstone. *Arbutus unedo* was absent from the woods, but richly present in waterside scrub.

Dr A. S. Watt, who was with the expedition, suggested that these Irish woods had close affinities with evergreen forest of similar climate in North America and was inclined to suggest the purely historical factor of the Ice Age as responsible for the absence of species which would be expected on this assumption.

Prof. Salisbury, Prof. Boycott and Dr Burtt Davy spoke in the discussion, and Dr Paul Richards continued with a description of the bryophytic communities of the same oakwoods. He recognized in each woodland type a series of moss communities from the tree tops downwards: (1) branches, (2) trunks, (3) forest floor, (4) boulders, (5) steep banks with no fallen leaves, (6) logs. In each habitat it was possible to distinguish a serule leading to a miniature climax. With increasing openness and exposure of the woodland types the moss communities came relatively closer to the ground.

Dr V. J. Chapman then read a paper on the salt marshes he had examined on the eastern coast of North America. He separated those of Nova Scotia, with a silt-like substratum, those of Maine and New Jersey with a "marine peat", and those south to Florida, with silt. He described the vegetation, stressing the severity of winter conditions as contrasted with those of British coasts, and gave evidence supporting Dawson's theory of origin of the New England marshes by subsidence. Interesting evidence was also produced of the rate of marsh growth. In the discussion which followed Dr Turrill and Mr Marchand took part.

Prof. Matthews expressed the warm appreciation felt by the Society of the kindness shown them by Profs. Salisbury and Hill in giving facilities for the meeting, and of the trouble taken by Prof. Salisbury and Dr Barbara Russell-Wells in organizing both meeting and soirée. The vote of thanks was carried with acclamation and the meeting adjourned at 4.30 p.m.

LIST OF MEMBERS (January 10th, 1937)

E.=Takes *The Journal of Ecology*. A.=Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, Dr H. Godwin, Botany School, Cambridge.

E. A. **Adams**, Dr Charles C.; New York State Museum, Albany, N.Y., U.S.A.
E. **Adamson**, Prof. R. S., M.A.; The University, Cape Town, S. Africa.
A. **Alexander**, W. B., M.A.; University Museum, Oxford.
E. **Allan**, Dr H. H.; Plant Research Institute, Palmerston North, N.Z.
A. **Allee**, W. C.; Zoology Building, University of Chicago, Chicago, Ill., U.S.A.
E. **Allorge**, Pierre; Laboratoire de Cryptogamie, 63, Rue de Buffon, Paris.
E. **Alun-Roberts**, R.; Agricultural Dept., University College, Bangor.
E. **Anand**, P. L., M.Sc.; Dept. of Biology, Sanatana Dharma College, Lahore, India.
E. **Andersonian Naturalists' Society** (cf. Glasgow).
E. A. **Arkwright**, J. A., M.D., F.R.S.; Lister Institute, Chelsea, London, S.W. 1.
E. **Armitage**, Miss E.; Dadnor, Ross, Herefordshire.
E. **Ashby**, Eric, B.Sc.; The University, Bristol.
E. **Bacon**, Mrs Alice; The Technical College, Brighton.
A. **Barber**, Miss E. G.; Harborne, Westbourne Avenue, Emsworth, Hants.
E. **Baker**, H.; University Dept. of Botany, High St., Oxford.
E. **Barnes**, Dr B.; 28, Torridon Road, London, S.E. 6.
A. **Barnes**, H. F., Ph.D.; Rothamsted Experimental Station, Harpenden, Herts.
E. **Bates**, G. H., B.Sc.; The Farm Institute, Penkridge, Stafford.
E. A. **Beauchamp**, R. S. A., B.A.; The Laboratory, Wray Castle, Ambleside.
E. **Bell**, Prof. H. P.; Dalhousie University, Halifax, Nova Scotia.
A. **Bertram**, G. C. L., B.A.; St Keyne, Berkhamsted, Herts.
E. A. **Bews**, Prof. J. W.; University College, Pietermaritzburg, Natal.
E. **Bharucha**, Dr F. R.; 6, Alexandra Road, New Gamdevi, Bombay 7.
E. **Blackburn**, K. B., D.Sc.; Armstrong College, Newcastle-upon-Tyne.
E. **Blackman**, G. E.; Wick Cottage, Westleigh Av., Putney Hill, London, S.W. 15.
A. **Blair**, H. M. S., M.B., B.S.; Thorney House, Laygate, S. Shields, Durham.
E. **Bloomer**, H. H.; Longdown, Sunnydale Road, Swanage, Dorset.
E. **Bor**, N. L., M.A., D.Sc.; Chardwar, Lokra, P.O., Balipara, Frontier Tract, Darrang, Assam.
E. **Børgesen**, Dr F. C. E.; Botanisk Museum, Gothersgade 130, Copenhagen.
E. **Borthwick**, Dr A. W.; 25, Drumsheugh Gardens, Edinburgh.
A. **Bosanquet**, S. J. A.; Dingeston Court, Monmouth.
E. A. **Boycott**, Prof. A. E., F.R.S.; Ewen Farm House, nr Cirencester.
A. **Boyd**, A. W., M.C., M.A.; Frandley House, nr Northwich, Cheshire.
E. **Boyd**, L.; Royal Botanic Gardens, Edinburgh.
E. **Bracher**, Miss Rose, Ph.D.; Dept. of Botany, The University, Bristol.
E. **Braid**, Major K. W.; 6, Blythswood Square, Glasgow.
E. **Braun**, Miss E. L.; 2702, May Street, Cincinnati, Ohio, U.S.A.
E. **Brenchley**, Dr Winifred E.; Rothamsted Experimental Station, Harpenden, Herts.
E. **Brodsky**, Prof. A.; Middle Asiatic State University, Tashkent, Usbekistan, U.S.S.R.
E. **Brooks**, Prof. F. T., M.A., F.R.S.; Botany School, Cambridge.
A. **Brown**, F. M.; Bryn-cliffe, Hungerford Road, Huddersfield, Yorks.

A. **Burnett**, Miss I. M.; Malvern Girls' College, Worcestershire.
E. **Burtt**, B. D.; Botanist, Tsetse Research, Shinyanga, Tanganyika Territory, E. Africa.
E. **Burtt Davy**, Dr J.; Imperial Forestry Institute, Oxford.
E. **Butcher**, R. W., B.Sc.; Fisheries Research Station, Alresford, Hants.
A. **Buxton**, Prof. P. A.; London School of Hygiene, Keppel Street, London, W.C. 1.
E. **de Caen**, Mrs, Ph.D.; Springfield, Delgany, Co. Wicklow, Ireland.
A. **Cameron**, A. E., D.Sc.; Dept. of Agricultural Zoology, The University, Edinburgh.
A. **Carpenter**, Prof. G. D. Hale, M.B.E., D.M.; Penguelle, Hid's Copse Road, Cumnor Hill, Oxford.
A. **Carpenter**, J. R., M.Sc.; Lincoln College, Oxford.
A. **Carpenter**, Prof. K. E., Ph.D.; 105, Front Street, Chestertown, Maryland, U.S.A.
A. **Carter**, Dr G. S.; Corpus Christi College, Cambridge.
E. **Carter**, Dr Nellie; E. London College, Mile End Road, London, E. 1.
E. **Chambers**, Miss W. E., B.Sc.; Innesbrook, Watlington, Oxon.
A. **Chapman**, Prof. R. N.; University of Hawaii, Honolulu, Hawaii.
E. **Chapman**, P. C.; Charterhouse School, Godalming, Surrey.
E. A. **Chapman**, V. J.; The Rectory, Alcester, Warwicks.
A. **Charlesworth**, R.; 190, Padgate Lane, Warrington.
A. **Charteris**, Hon. Guy; 24, Oxford Square, London, W. 2.
A. **Chitty**, D. H.; Bureau of Animal Population, University Museum, Oxford.
E. **Clapham**, Dr A. R.; Botanical Dept., The University, Oxford.
E. A. **Clements**, Prof. F. E.; Mission Canyon, Santa Barbara, California.
A. **Cohen**, E.; 86, Major Street, Manchester.
E. **Colville**, Miss E. G.; Arngomery, Kippen, Stirlingshire, Scotland.
A. **Corley**, H. V.; Hyron's Lodge, Amersham, Bucks
E. **Conway**, Miss V. M.; 61, De Freville Avenue, Cambridge.
E. **Cooper**, Prof. W. S.; Dept. of Botany, University of Minnesota, Minneapolis, Minn.
E. **Cotton**, A. D.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Cowles**, Prof. H. C.; University of Chicago, Chicago, Ill., U.S.A. (*Hon. Life Member*).
A. **Crosthwaite**, J. M.; 207, West George Street, Glasgow.
E. **Croydon Natural History and Scientific Society**, 27, High Street, Croydon.
E. **Curtis**, Miss W. M., B.Sc.; 12, Blenheim Road, Caversham, Reading, Berks.
E. **Cutting**, E. M., M.A.; 125, Tredegar Road, Bow, London, E.
A. **Dalgety**, C. T.; Denver Hall, Downham Market, Norfolk.
A. **Darling**, F. F., Ph.D.; Brae House, Dundonnell, by Garve, Wester Ross, Scotland.
E. **Davey**, Miss A. J., M.Sc.; University College of N. Wales, Bangor, N. Wales.
E. **Davies**, W. C.; The Cawthron Institute, Nelson, N.Z.
A. **Davis**, D. H. S.; University Museum, Oxford.
E. **Davis**, T. A. W.; Forestry Dept., Mazaruni Station, British Guiana.
E. **Dawson**, R. B., M.Sc., F.L.S.; St Ives Research Station, Bingley, Yorks.
E. **Deam**, C. C.; Bluffton, Indiana, U.S.A.
E. **Delf**, Dr E. M.; Westfield College, Hampstead, London, N.W. 3.
A. **Diver**, C.; 40, Pembroke Square, Kensington, London, W. 8.
E. **Dowling**, Miss R. E., M.Sc.; The Nest, Ledgers Road, Slough, Bucks.
A. **Duncan**, A. B., B.A.; Gilchristland, Closeburn, Dumfries.
E. **Du Rietz**, Prof. Einar; Vaxtbiologiska Institutionen, Upsala, Sweden.
E. A. **Dyke**, F. M., B.Sc.; Branksome, Boreham Woods, Herts.
E. **Eden**, T.; Tea Research Institute, St Coombs, Talawakelle, Ceylon.
E. A. **Eggeling**, W. J., B.Sc.; Forest Office, Entebbe, Uganda.
E. **Ekblaw**, Dr W. E.; Clark University, Worcester, Mass., U.S.A.
A. **Ellis**, R.; 2420, Ridge Road, Berkeley, California, U.S.A.

E. A. **Elton**, Charles; Bureau of Animal Population, University Museum, Oxford (*Hon. Editor of The Journal of Animal Ecology*).

E. **Essex Field Club, The** (Essex Museum of Natural History, Romford Road, Stratford, Essex).

A. **Eyre**, Miss J.; Dept. of Zoology, University of Cape Town, S.A.

E. **Evans**, E. Price; White Broom, 69, Westgate, Hale, Cheshire.

A. **Evans**, F. C.; Oriel College, Oxford.

E. **Evans**, G. C.; Botany School, Cambridge.

E. **Falk**, P.; 24, Rokeby House, Rugby.

E. A. **Featherly**, Prof. H. I.; Oklahoma Agricultural and Mechanical College, Stillwater, Okla., U.S.A.

E. **Fenton**, E. Wyllie; 13, George Square, Edinburgh.

A. **Fidler**, J. H.; Dept. of Agricultural Entomology, Victoria University, Manchester.

E. **Fisher**, H. S., M.Sc.; University College, Oxford.

A. **Fisher**, J. M. Mc.; Magdalen College, Oxford.

E. A. **Fitzgerald**, D. V.; Clammer Hill, Haslemere, Surrey.

E. **Foggie**, A., B.Sc.; c/o Conservator of Forests, Forestry Department, Accra, Gold Coast, Africa.

A. **Ford**, J.; New College, Oxford.

E. **Fraser**, G. K., M.A., B.Sc.; Forestry Dept., Marischal College, Aberdeen.

E. **Fritsch**, Prof. F. E., F.R.S.; Pilgrim's End, West Humble, Dorking.

E. **Fuller**, Prof. G. D.; Botany Dept., The University, Chicago, Ill., U.S.A.

E. **Galloway**, J. A.; Oak Bank, Bowness on Windermere, Westmorland.

E. **Gams**, Dr H.; Innsbruck-Hotting, Schreeburggasse 67, Austria.

E. A. **Garner**, J. H., B.Sc.; West Riding Rivers Board, 71, Northgate, Wakefield.

E. **Gibson**, Miss C. M.; The Municipal College, Portsmouth.

A. **Gilbert**, H. A., B.A.; Bishopstone, Hereford.

E. **Gilbert-Carter**, H., M.A., M.B.; Cory Lodge, Botanic Garden, Cambridge.

E. **Gillman**, H., M.Sc.; District Agricultural Office, Bukoba, Tanganyika Territory.

E. **Gilmour**, J. S. L., B.A.; Royal Botanic Gardens, Kew, Surrey.

E. A. **Glasgow and Andersonian Nat. Hist. and Microscopic Soc.**; Societies' Rooms, Royal Technical College, Glasgow.

E. A. **Godwin**, H., Ph.D.; Botany School, Cambridge (*Hon. Secretary*).

E. A. **Good**, R. D'O.; University College, Hull.

E. **Gourlay**, W. B., M.A., M.B.; 7, Millington Road, Cambridge.

E. **Griffith Tedd**, H.; P.O. Box 30, Xanthie, Greece.

E. A. **Griffiths**, B. M., D.Sc.; Dept. of Botany, University Science Labs., South Road, Durham.

A. **Gurney**, Dr R.; Bayworth Corner, Boar's Hill, Oxford.

E. **Halket**, Miss A. C., B.Sc.; Bedford College, Regent's Park, London, N.W. 1.

E. **Halliday**, W. E. B.; c/o Dominion Forest Service, 813, New Federal Building, Winnipeg, Manitoba, Canada.

E. A. **Hancock**, G. L. R.; Makenene College, Box 262, Kampala, Uganda.

E. **Hands**, Mrs, B.Sc.; Beachfield, The Folly, Radlett, Herts.

E. **Hanson**, Dr Herbert C.; Botanist and Head of Dept. of Botany, North Dakota Agric. College and Expt. Station, Fargo, North Dakota, U.S.A.

A. **Hardy**, Prof. A. C., M.A.; University College, Hull.

E. **Hare**, C. Leighton, B.Sc.; Department of Botany, The University, Aberdeen.

A. **Hare**, Prof. T., M.D.; 70, Holywell Hill, St Albans.

A. **Harris**, W. V.; Dept. of Agriculture, Morogoro, Tanganyika Territory.

E. **Harris**, C. M.; Forest Office, Sutebbe, Uganda.

E. **Harrison**, A. B.; The Hollies, Farndon, Newark-on-Trent.

A. **Harvey**, A. L., M.Sc.; Dept. of Zoology, University College of S.W. England, Exeter, Devon.
E. **Heddle**, R. G., M.A., B.Sc.; Edinburgh and E. of Scotland College of Agric., 13, George Square, Edinburgh.
E. **Hewetson**, C. E.; Indian Forestry Service, Jubbulpur, Central Provinces, India.
E. **Hilary**, Miss D., B.Sc.; 15, Plevna Terrace, Bingley, Yorks.
E. **Hill**, Sir A. W., F.R.S.; Royal Botanic Gardens, Kew, Surrey.
E. **Hill**, Prof. T. G.; University College, London, W.C. 1.
A. **Hobby**, B. M., M.A., D.Phil.; University Museum, Oxford.
E. **Holch**, Dr A. E.; Botany Dept., University of Denver, Colorado, U.S.A.
E. **Hole**, D. R., B.Sc.; Rousdon, Cutbush Lane, Shinfield, Reading.
E. **Holttum**, R. E., M.A.; The Botanic Gardens, Singapore.
E. **Horne**, F. R.; Seale-Hayne Agric. College, Newton Abbot, Devon.
E. **Howarth**, W. O.; Botany Dept., The University, Manchester.
E. **Hubbard**, C. E.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Hugh-Jones**, E.; King's College, Cambridge.
A. **Huntingdon**, E.; Dept. Geological Sciences, 4, Hillhouse Avenue, New Haven, Connecticut, U.S.A.
E. **Hutchinson**, R. R.; 11, Fryston Avenue, Croydon.
E. **Hyde**, H. A., M.A.; National Museum of Wales, Cardiff, S. Wales.
A. **Imms**, D. A., D.Sc.; Zoological Dept., Cambridge.
A. **Jackson**, C. H. N., Ph.D.; Dept. of Tsetse Research, Shinyanga, Tanganyika Terr.
E. **Jennings**, A. E.; Carnegie Museum, Pittsburg, Pa., U.S.A.
E. **Joaquim**, Miss U. I. A., B.Sc.; Woodhall Girls' School, Woodhall Spa, Lincs.
E. **Jones**, E. W.; Imperial Institute of Forestry, Oxford.
E. **Jones**, Miss G. M.; The Cottage, Wraysbury, Bucks.
A. **Kay**, G. T.; 51 St Olaf Street, Lerwick, Shetland Is.
E. **Kashkarov**, Prof. D.; Tashkent, Novaia 19, Usbekistan, U.S.S.R. (Russia).
E. **Kawada**, Prof.; Forest Experiment Station, Shimomeguro Meguro, nr Tokio, Japan.
E. A. **Kendeigh**, S. C., Ph.D.; Experimental Zoology Laboratory, University of Illinois, Wright and Healey Stations, Champaign, Illinois.
E. **Kessell**, S. L.; Conservator of Forests, Forests Dept., Perth, W. Australia.
A. **Kitching**, J. A., B.A.; Birkbeck College, Fetter Lane, London, E.C. 4.
A. **Lack**, D.; The School, Dartington Hall, Totnes.
A. **Latter**, O. H.; The Elms, Charterhouse Road, Godalming, Surrey.
E. **Laughton**, F. S.; Assistant Forest Officer, Concordia, Knysna, C.P., S. Africa.
E. **Leach**, W.; The University, Edgbaston, Birmingham.
A. **Lemon**, F. E.; Royal Society for Protection of Birds, 82, Victoria Street, London, S.W. 1.
A. **Lewis**, D. J., M.A.; Shenfield Rectory, Brentwood, Essex.
E. **Lewis**, Prof. F. J.; University of Alberta, Edmonton, Alberta, Canada.
E. **Lind**, Miss E. M., B.Sc., Ph.D.; The University, Sheffield.
E. A. **London Natural History Society**; c/o L. Parmenter, 94, Fairlands Avenue, Thornton Heath, Surrey.
A. **Longstaff**, Dr T. G., M.A., D.M.; Picket Hill, Ringwood, Hants.
E. A. **Lowndes**, A. G., M.A., F.L.S.; Marlborough College, Wilts.
E. **Lüdi**, Dr W.; Mohrlistrasse 93, Zurich, Switzerland.
A. **MacLaglan**, D. S.; Nat. Hist. Dept., Marischal College, Aberdeen.
A. **MacLeod**, J., Ph.D.; The Cooper Field Research Station, Little Gaddesden, Berkhamsted, Herts.
A. **MacLulich**, D. A.; Royal Ontario Museum of Zoology, Queen's Park at Bloor Street, Toronto, Canada.

E. A. **McBeath**, D. K.; Ballochyle House, Sandbank, Argyllshire.
E. **McLean**, Prof. R. C.; University College, Cardiff, S. Wales.
E. **McLuckie**, J., D.Sc.; Dept. of Botany, The University, Sydney, N.S.W
E. **Mangham**, Prof. S., M.A.; University College, Southampton.
A. **Marples**, B. J.; Zoology Dept., The University, Bristol.
E. **Marquand**, C. V. B., M.A.; Langdale, 46, Hook Rise, Tolworth, Surrey.
E. **Marsden-Jones**, E. M.; The Potterne Biological Station, nr Devizes, Wilts.
E. **Martin**, J. D.; Assistant Conservator of Forests, Lusaka, N. Rhodesia.
A. **Matheson**, C.; Dept. of Zoology, National Museum of Wales, Cardiff.
E. **Mason**, E. W.; Inglenook, 63, King's Road, Richmond, Surrey.
E. **Matthews**, Prof. J. R., M.A.; The University, Old Aberdeen.
A. **Meynele**, M.; Hoar Cross, Burton-on-Trent, Staffs.
E. A. **Michelmore**, A. P. G., B.A.; Saffron Close, Chudleigh, S. Devon.
A. **Middleton**, A. D.; University Museum, Oxford.
E. A. **Middleton**, A. R.; Biological Labs., University of Louisville, Louisville, Kentucky, U.S.A.
Miller, W. B.; Sojourner's Club, Fort Bayard, New Mexico, U.S.A.
E. A. **Milne-Redhead**, E., M.A.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
A. **Mitchell** M. V.; Grayrigg, Old Colwyn, N. Wales.
E. **Misra**, R. D.; The Laboratory, Wray Castle, Ambleside.
E. **Mohan**, N. P., M.A.; c/o Lloyds Bank, The Mall, Lahore, Punjab, India.
A. **Mohr**, C. O.; State Natural History Survey, Urbana, Illinois, U.S.A.
A. **Montford**, H. M., B.Sc.; Armina, Petersham Road, Richmond, Surrey.
A. **Moon**, H. P., B.A.; Dept. of Zoology, University College, Southampton.
E. **Mooney**, H. F., M.A.; Ranchi, B.N. Railway, India.
E. A. **Moore**, Barrington; Stone Acre, Corfe, Taunton.
E. **Moore**, E. J.; Central Technical College, Birmingham.
E. **Murray**, J. M., B.Sc.; 76, Hillview Terrace, Corstorphine, Edinburgh, 12.
E. A. **Newman**, Leslie F., M.A.; St Catharine's College, Cambridge.
E. A. **Newton**, Prof. Lily, M.Sc., Ph.D.; Dept. of Botany, University College of Wales, Aberystwyth, Wales.
E. **Nichols**, Prof. G. E.; Botany Dept., Yale University, New Haven, Conn., U.S.A.
A. **Nichols**, J. E., Ph.D.; Dept. of Agric., University of W. Australia, Crawley.
A. **Nicholson**, E. M.; 61, Marsham Street, London, S.W. 1.
E. A. **Nurse**, H. P.; 13, Haggard Road, Twickenham, Middlesex.
E. **Ogg**, W. G., M.A., Ph.D.; Macaulay Inst. for Soil Research, Craigiebuckler, Aberdeen.
E. A. **Oldham**, Charles; The Bollin, Shrublands Road, Berkhamsted, Herts.
E. **Oliver**, Prof. F. W., F.R.S.; Burg-el-Arab, Mariut, Egypt.
E. A. **Oliver**, W. R. B., D.Sc.; Dominion Museum, Wellington, N.Z.
E. **Olmsted**, C. E.; Dept. of Botany, University of Chicago, U.S.A.
A. **Omer-Cooper**, Prof. J., M.A., M.Sc.; Armstrong College, Newcastle-upon-Tyne.
E. **Orr**, M. Y.; Royal Botanic Gardens, Edinburgh.
E. **Osborn**, Prof. T. G. B.; Dept. of Botany, Sydney University, Sydney, N.S.W.
E. A. **Park**, Dr O.; Zoological Dept., University of Illinois, Urbana, Ill., U.S.A.
E. **Peace**, T. R., M.A.; Imperial Forestry Institute, Oxford.
A. **Peacock**, Prof. A. D., D.Sc., F.R.S.E.; University College, Dundee.
E. A. **Pease**, I. E., The Hollins, Ramton, Northallerton.
E. **Pearsall**, W. H., D.Sc.; Botany Dept., The University, Leeds (*President*).
A. **Pentelow**, F. T. K.; Fisheries Research Station, Alresford, Hampshire.
A. **Percival**, E.; Canterbury College, Christchurch, New Zealand.
E. A. **Perthshire Soc. of Nat. Science** (Secretary, John Ritchie); Perthshire Soc. of Nat. Science Museum, Perth, Scotland.

E. **Petch**, C. P.; Sundial House, North Wootton, King's Lynn, Norfolk.
Phillips, P. G.; Box 605, Gallup, New Mexico, U.S.A.
E. **Phillips**, Prof. J. F. V., D.Sc.; University of Witwatersrand, Milner Park, Johannesburg, Transvaal.
A. **Pickles**, W.; 23, Beech Grove Avenue, Garforth, Leeds, Yorks.
E. **Pilling**, M., Ph.D.; Croft House, Outlane, Huddersfield.
A. **Pitt**, Miss F.; The Albynes, Bridgnorth, Salop.
E. **Pitt-Schenkel**, J.; c/o Forest Dept., Morogoro, Tanganyika Territory.
E. **Pledge**, H. T.; 10^6 West Bolton Gardens, London, S.W. 5.
A. **Plomley**, N. J. B.; c/o Bank of New South Wales, 29, Threadneedle Street, London, E.C. 2.
A. **Pollitt**, G. P., Col.; Harrage Grange, Cressage, Shropshire.
E. **Polunin**, N., Ph.D.; Univ. Dept. of Botany, High Street, Oxford.
E. **Powell**, Miss Doris, M.Sc.; Aldersyde, Reigate, Surrey.
E. A. **Praeger**, Dr R. Lloyd; Royal Irish Academy, 19, Dawson Street, Dublin.
E. **Price**, W. R.; Cockleford Mill, Cowley, Nr Cheltenham.
E. **Priestley**, Prof. J. H., B.Sc.; The University, Leeds.
E. **Ramsbottom**, J., M.A., O.B.E.; Botanical Dept., British Museum (Nat. History), London. S.W. 7.
A. **Ratcliffe**, F. N., B.A.; Nat. History Dept., Marischal College, Aberdeen.
E. **Rayner**, Dr M. C.; Bedford College, University of London, Regent's Park, London, N.W. 1.
E. **Rees**, T. Kenneth; University College, Singleton Road, Swansea, S. Wales.
E. **Rees**, J., B.A., B.Sc.; University College, Cardiff.
E. **Regel**, Prof. Constantin; The Botanical Garden, Kaunas (Kovno), Lithuania.
A. **Reid**, D. M.; Science Schools, Harrow-on-the-Hill, Middlesex.
E. A. **Renouf**, Prof. L. P. W.; University College, Cork, I.F.S.
E. **Rice**, C. H., B.Sc. Ph.D.; 20, Dyson Road, Leytonstone.
E. A. **Richards**, O. W., M.A., D.Sc.; 29 *a*, Edith Road, London, W. 14.
E. **Richards**, P. W.; The Botany School, Cambridge.
A. **Ritchie**, Prof. J., M.A., D.Sc.; Marischal College, Aberdeen.
Ritson, Miss K. E.; 199, Maidstone Road, Rochester, Kent (*Associate Member*).
E. **Robertson**, R. N.; The Botany School, Cambridge.
E. A. **Robbins**, Prof. C. R., M.C., M.A.; c/o Messrs Lloyds Bank, 6, Pall Mall, London, W. 1.
A. **Roberts**, B. B.; Bishopsgarth, Woking, Surrey.
A. **Roberts**, J. I.; Medical Research Lab., Box 141, Nairobi, Kenya Colony.
E. **Rogers**, Miss M. H., Green Bank, Four Oaks, Warwicks.
E. **Ross**, R.; Botany School, Cambridge.
E. **Rübel**, Dr E.; Zürichbergstrasse 30, Zürich, Switzerland.
A. **Rushton**, W., D.Sc.; Biological Dept., St Thomas's Hospital Medical School, Albert Embankment, London, S.E. 1.
A. **Russell**, Dr E. S.; Dolphins, Northchurch Common, Berkhamsted, Herts.
E. **Russell-Wells**, Miss B., Ph.D.; Botany Dept., University College, London, W.C. 1.
E. **Sager**, J. L., M.A.; University College, Exeter.
E. A. **Salisbury**, Prof. E. J., F.R.S.; Willow Pool, Radlett, Herts (*Vice-President*).
E. **Sandwith**, N. Y., M.A.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Saunders**, Miss E. R.; 37 Millington Road, Cambridge.
E. A. **Saunders**, J. T., M.A.; Christ's College, Cambridge.
A. **Savage**, R. M.; 19, Derwent Avenue, London, N.W. 7.
E. **Schröter**, Prof. C.; Seegartenstrasse, Pensionseegarten, Zürich 8, Switzerland (*Hon. Life Member*).
A. **Scourfield**, D. J., I.S.O., F.L.S.; 6, Chadwick Road, Leytonstone, London, E. 11.

Selwood, Miss G. F.; 49, Blenheim Road, Moseley, Birmingham (*Associate Member*).

E. **Sernander**, Prof. R.; Vaxtbiologiska Institutionen, Upsala, Sweden.

A. **Severtzeff**, Dr S. A.; Zoological Museum, M.G.U., Moscow, U.S.S.R.

E. **Shantz**, Pres. H. L.; Forest Service, Washington, U.S.A.

E. A. **Shelford**, Prof. Victor E.; Vivarium Building, Wright and Healey Streets, Champaign, Ill., U.S.A.

E. **Sherrin**, W. R.; South London Bot. Inst., 323, Norwood Road, Herne Hill, London, S.W. 24.

E. **Shirk**, C. J., Ph.D.; Nebraska Wesleyan University, Lincoln, Nebraska, U.S.A.

A. **Shorrock**, W. G.; Morland Hall, nr Penrith, Westmorland.

E. **Singh**, Prof. B. N., D.Sc.; Institute of Agricultural Research, Benares Hindu University, Benares, India.

E. **Skene**, Prof. Macgregor, D.Sc.; The University, Bristol.

E. **von Soò**, Prof. Rudolf; Debrécen, Hungary.

E. **Sperrin-Johnson**, Dr J. C.; Botany Dept., University College, Cork.

E. **Sprague**, T. A., D.Sc.; Royal Botanic Gardens, Kew, Surrey.

E. A. **Stamp**, Dr L. Dudley; London School of Economics, London, W.C. 2.

E. **Stapledon**, Prof. R. G., M.A., C.M.G.; University College, Aberystwyth.

A. **Stephenson**, Prof. T. A., D.Sc.; The University, Rondebosch, Cape Town, S. Africa

E. **Stevenson**, Miss E. H.; The Training College, The Close, Salisbury.

E. A. **Steward**, F. C., Ph.D.; Dept. of Botany, Birkbeck College, Bream's Buildings, Fetter Lane, London, E.C. 4.

E. **Stiles**, Prof. W., M.A., F.R.S.; The University, Birmingham.

A. **Storrow**, B., M.Sc.; Dove Marine Lab., Cullercoats, Northumberland.

E. **Summerhayes**, V. S., B.Sc.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.

E. **Swabey**, C.; Forest Department, Port of Spain, Trinidad, B.W.I.

A. **Swynnerton**, C. F. M., Department of Tsetse Research, Shinyanga, Tanganyika Territory.

A. **Swynnerton**, G. H.; c/o Messrs Grindlay and Co. Ltd., 54, Parliament Street, London, S.W. 1.

E. **Symington**, C. F., Kepong, Selangor, Federated Malay States.

E. **Synge**, P. M.; Clare Cottage, West Byfleet, Surrey.

E. A. **Tansley**, Prof. A. G., F.R.S.; Grantchester, Cambridge; and Magdalen College, Oxford (*Hon. Editor of The Journal of Ecology*).

E. **Thoday**, Prof. D., M.A.; University College, Bangor, N. Wales.

E. **Thomas**, Dr Ethel Miles; University College, Leicester.

E. **Thomas**, H. Hamshaw, Sc.D., F.R.S.; Botany School, Cambridge.

E. **Thompson**, H. Stuart, A.L.S.; 11, Buckingham Place, Clifton, Bristol.

E. **Thompson**, Prof. J. McLean; Botanical Dept., The University, Liverpool.

E. **Tidmarsh**, C. E. M.; Clare College, Cambridge.

E. **Tincker**, M. A. H., D.Sc.; Royal Horticultural Society Gardens, Ripley, Wisley, Surrey.

E. **Topham**, P., M.A.; Dedza, Nyasaland, B.C., Africa.

E. A. **Trapnell**, C. G., B.A.; Department of Agriculture, Mazabuka, N. Rhodesia.

A. **Tucker**, B. W., M.A.; 9, Marston Ferry Road, Oxford.

E. **Turner**, J. S., Ph.D.; 2, Drosier Road, Cambridge.

E. A. **Turrill**, W. B., D.Sc.; Royal Botanic Gardens, Kew, Surrey (*Vice-President*).

E. **Tutin**, T. G., B.A.; The Botany School, Cambridge.

A. **Uéno**, M.; Otsu Biological Station of the Kyoto Imperial University, Shigaken, Japan.

A. **Uvarov**, B. P.; British Museum (Nat. History), London, S.W. 7.

E. **Valentine**, D. H.; The Botany School, Cambridge.

A. **Varley**, G. C., B.A.; Sidney Sussex College, Cambridge.
E. **Vaughan**, R. E., B.Sc., A.R.C.S.; Royal College, Cure Pipe, Mauritius.
A. **Venables**, L. S. V.; The Moors, Tilford, Surrey.
E. **de Vesian**, Miss D. E.; Ladies' College, Cheltenham.
A. **Volterra**, Prof. V., D.Sc., LL.D.; Via in Lucina 17, Roma, Italy.
E. **Vyvyan**, M. C., M.A.; Trevedran, Wateringbury, Kent.
E. **Wadham**, Prof. S. M.; School of Agriculture, Melbourne University, Victoria, Australia.
A. **Waite**, Miss B. E.; Museum Cottage, Haslemere, Surrey.
A. **Waloff**, Miss N.; Clevelands, Benenden, Cranbrook, Kent.
E. **Walton**, Prof. J.; Dept. of Botany, The University, Glasgow.
E. **Wangerin**, Prof. W.; Danzig Langführ, Am Heiligenbrunn 4, Danzig.
A. **Warwick**, T., B.Sc.; Royal (Dick) Veterinary College, Edinburgh.
E. **Watson**, W., D.Sc.; Cedene, Chaddon Road, Taunton, Somerset.
E. A. **Watt**, A. S., Ph.D.; The Botany School, Cambridge.
A. **Watt**, Hugh Boyd; 90, Parliament Hill Mansions, Lissenden Gardens, N.W. 5 (*Hon. Treasurer*).
E. A. **Weese**, Prof. A. O.; University of Oklahoma, Norman, Okla., U.S.A.
A. **Weiss**, Prof. F. E., F.R.S.; Easedale, Woodway, Merrow, Guildford.
A. **White**, K. M., B.Sc.; Glastonbury, Boyn Hill Avenue, Maidenhead.
E. **Wiehe**, P. O.; Phoenix, Mauritius.
A. **Williams**, C. B.; Rothamsted Experimental Station, Harpenden, Herts.
E. **Wilmott**, A. J., M.A.; Botanical Dept., British Museum (Nat. History) London, S.W. 7.
E. **Woodhead**, Norman; University College, Bangor, N. Wales.
E. **Woodhead**, Dr T. W.; The Willows, 35, Longley Road, Huddersfield.
E. **Wright**, N., A.R.C.S., B.Sc.; Imperial College of Tropical Agriculture, St Augustine, Trinidad, B.W.I.
A. **Yapp**, W. B., B.A.; The Grammar School, Rusholme, Manchester.
E. A. **Yoshii**, Prof. Y.; Inst. of Biology, Tohoku Imperial University, Sendai, Japan.